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Chimpanzee personality and its relations with cognition and health: a comparative perspective

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Declaration

I hereby declare that this thesis is of my own composition, and that it contains no material previously submitted for the award of any other degree. The work reported in this thesis has been executed by myself, except where due acknowledgement is made in the text.

Signed,

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A Note on Personal Pronouns

This thesis is based to a large extent on published work and work under review. In order to maintain consistency with the published literature, and to acknowledge the collaborative nature of the work, “we” rather than “I” is used throughout.

Abstract

This thesis aimed to address two main questions. First, considering that personality is frequently associated with cognitive abilities in humans, do chimpanzees' personalities and cognitive capacities covary in ways similar to what is observed in humans, as well as older evolutionary cousins, rhesus macaques? Second, given that human and animal personality have previously been shown to relate to health and longevity, does personality in chimpanzees also relate to various measures of health?

Chapter 1 provides an introduction to and brief history of comparative personality psychology, particularly in the context of intelligence research and psychosomatic medicine.

Chapter 2 describes three studies with a group of 19 zoo-housed chimpanzees who interacted with touchscreen tasks over the course of 3 years of research. We found that high Conscientious chimpanzees were more likely to stick with the tasks, and performed better as a results, but once their extra experience was taken into account, their performance advantage disappeared. However, we also found associations between better interest and performance with high Openness, high Extraversion, and low Agreeableness.

In Chapter 3 we examine performance in conjunction with personality, with 9 rhesus macaques. The macaques also engaged with touchscreen tasks, but were expert subjects and displayed plateau performance. We found consistent associations between many measures of performance and both high Openness and high Friendliness (which is similar to Extraversion).

With Chapter 4 we transition to our studies of personality and health. Chapter 4 examines personality and longevity in a sample of 538 personality rated, captive chimpanzees. These chimpanzees were followed for between 6 and 23 years after being rated. We found that high Agreeableness chimpanzees were more likely to live longer, but no other personality traits had a significant impact on longevity.

In Chapter 5, we compared biomarkers from samples of 177 chimpanzees housed at the Yerkes National Primate Research Centre, and 29,314 humans from the National Health and Nutrition Examination Survey. Both samples had been tested for the most common haematological and metabolic blood biomarkers, and we used these to assess stress in the form of allostatic load, between species. We found a similar structure of biomarkers in across humans and chimpanzees.

In Chapter 6, we took our allostatic load measure from chapter 5 and looked at how it was associated with personality, in the same chimpanzee sample from the Yerkes Primate Centre, and in the longitudinal Midlife in the United States and Midlife in Japan biomarker study samples, which consisted of 993 and 382 individuals, respectively. We found that Agreeableness was associated with allostatic load in both human samples, whereas Dominance was associated with allostatic load in chimpanzees.

Finally, Chapter 7 summarises the results presented in these five empirical chapters, and places our findings in the context of the existing literature. We discuss the limitations of the research, and offer some suggestions for future study.

Lay Summary

This thesis made two particular inquiries into the field of comparative personality psychology. First, are the dimensions of primate personality and cognitive ability associated with one another? If so, how? Considering the extensive positive evidence that has been reported in the human literature, we predicted that we would find similar associations in chimpanzees, and also macaques, though to a lesser extent. We studied both chimpanzee and rhesus macaque groups, collecting data on personality, cognitive performance, and participation in tasks, ultimately finding similarities in the relationships between personality, participation, and performance across species. Second, given that human and animal personality have previously been shown to relate to health and longevity, we investigated whether personality in chimpanzees is related to both mortality and stress, the latter of which we assessed using the results of several different blood tests. We found little consistency between the personality dimensions predicting higher stress and earlier mortality, but robust associations between several different personality dimensions and individual life outcomes. In these associations, we found some consistency with what has been reported for humans, as well as some effects that are distinctly chimpanzee. Overall, this thesis demonstrates the utility of personality to these types of experiments and analyses, particularly in large, well-powered studies.

Contents

1 Individual differences in comparison

1.1 The development of a differential psychology of primates

Personality and intelligence are the two most studied individual psychological differences, and research on these individual differences have produced results which are arguably the most reproducible in psychology (Chamorro-Premuzic & Furnham, 2006). Intelligence and personality share more features in common as well. Both describe cognitive, behavioral, and affective individual differences, which are quantified using standard psychometrics (Funder, 2001). Both intelligence and personality are, to differing extents, genetically influenced (Spinath & Johnson, 2011). Intelligence and personality also tend to be stable over an individual's lifetime (Caspi, 2000; Deary, Whalley, Lemmon, Crawford, & Starr, 2000), and both are associated with differences in outcomes, such as education (Poropat, 2009), health, and longevity (Calvin, Batty, & Deary, 2011).

Nevertheless, there are key differences between intelligence and personality. Intelligence is usually defined by maximal performance on tasks (see section 1.1.1), whereas personality captures broad tendencies in behavior (Cronbach, 1949). Put simply, intelligence is what an individual can do, and personality is what they typically do. Thus, intelligence and personality are assessed with quite different instruments, and validated using different criteria. In this section, we will begin with an overview of the evolution of these constructs, to understand their interrelationships, in humans, and in other species.

1.1.1 Intelligence

The empirical study of intelligence arguably began with Binet and Simon (1905), who described a set of higher order mental tests that could be administered to children of various ages in an effort to predict academic success or failure. Their goal was to provide an estimate of individual differences in intellectual ability, as opposed to ability gained through experience, social privilege, or other confounds of socioeconomic status (Binet & Simon, 1908). Their method employed a large battery of tests that focused on attention, memory, and other cognitive abilities (Binet & Simon, 1916). Their paradigm, which became foundational for the study of intelligence, rested on several crucial principles (Terman, 1916):

1. Tests should tap higher order cognitive abilities.
2. The effects of past experience and knowledge on test performance should be minimized as much as possible.
3. Participants should be instructed or otherwise compelled to exert maximal effort on tests.
4. Test performance should be validated. Typically, this is done by relating performance to academic achievement.

Binet and Simon's scales were designed for children, but later studies took inspiration from their work, and developed intelligence tests for adults. Some of the first adult intelligence tests were designed and applied by Robert Yerkes and his colleagues. Yerkes, Bridges, and Hardwick (1915) developed adult mental tests for use by the US military. These were the Army Alpha and Beta Examinations, and they were used to assess more than 1,700,000 men, making their effort the first adult

intelligence survey of this scale. Yerkes was a researcher with broad interests, and we will return to his work later.

Intelligence tests saw greater use in subsequent decades, particularly in educational contexts. Thorndike (1920) developed College Entrance Tests, which changed over time, but eventually found their way into higher educational systems (e.g. Scholastic Aptitude Test, American College Test). Standardized testing, though controversial, is now widely used at many levels of education, throughout the world (Haney, 1981), and have shown to effectively measure intelligence (Koenig, Frey, & Detterman, 2008).

As the field of intelligence research developed over the course of the 20th century, a consensus emerged on the structure of cognitive abilities. These abilities display a 'positive manifold', that is, scoring high on one test tends to indicate that an individual will score high on others (Spearman, 1925). This is true across virtually all cognitive tests, indicating the presence of a general intelligence factor, also known as *g* (Carroll, 1993; Spearman, 1925), that influences the entire span of human cognitive abilities. However, the best model for these many abilities is hierarchical with *g* sitting at the top (Holzinger & Swineford, 1939). Beneath *g*, second and third order factors reside, such as visual perception and mathematical reasoning (Gustafsson, 1984). These factors allow for individual variation in specific abilities, but they are oblique, i.e. correlated, which maintains the presence of an overall intelligence captured by *g*.

1.1.1.1 The primate perspective

Much primate cognition research is focused on understanding the highest achievements of apes and monkeys, and involve studying only a few subjects. Researchers train their subjects rigorously and extensively, driving them to learn and display abilities, which are impressive, and occasionally unmatchable. For example, Ayumu and other members of Project Ai display numeral chaining abilities that no human could perform (Inoue & Matsuzawa, 2007). If the goal is to show that a species is capable of mastering a particular task, then studying the extreme aptitudes of select individuals can be informative. However, the conclusions of these studies rely on the assumption that the task is a valid indicator of an underlying cognitive ability, and that the ability exists in the species in the first place. What we have established from test theory is that a single test is not likely to be reliable, hence the use of batteries in human intelligence testing. If the goal is to understand the average or range of capacities in a species, then the issues inherent to studies of small samples are compounded.

To study the variation of cognitive ability in animals, we need to determine how to operationalize this ability. Can cognitive ability be captured with one central domain, or many? Do many domains tap into a common, shared aptitude? As mentioned, research in humans (Carroll, 1993) supports this model with multiple correlated domains. However, evidence from other species is mixed, and even within chimpanzees, the structure of intelligence is not yet clear (Herrmann, Hernández-Lloreda, Call, Hare, & Tomasello, 2010; Hopkins, Russell, & Schaeffer, 2014).

Researchers and theorists have often posited that two domains of intelligence exist in apes: social and physical (Bluff, Weir, Rutz, Wimpenny, & Kacelnik, 2007;

Cheney, Seyfarth, & Silk, 1995; Penn, Holyoak, & Povinelli, 2008; Penn & Povinelli, 2007; Povinelli & Vonk, 2004; Tomasello & Call, 1997). Some investigations of the social domain involve observing and interpreting another's behavior, such as one's ability to follow another's gaze, and understand cues communicated by another to indicate the location of a reward (Tomasello, Call, & Hare, 1998). With the physical domain, researchers have questioned subjects' understanding of causality, quantity, and space. Relevant studies have required that subjects implement a variety of problem solving tasks, e.g., tasks which necessitate tool use to retrieve an out of reach object or keep track of a reward after the location has been changed (Albiach-Serrano, Call, & Barth, 2010; Povinelli, 2000).

Chimpanzee social cognitive abilities and tool-use abilities were the focus of a particular study, and compared directly with the performance of bonobos, orangutans, and young children (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Herrmann, Hare, Call, & Tomasello, 2010; Herrmann, Hernández-Lloreda, et al., 2010) Chimpanzees in particular are an important candidate for these investigations, for they are one of humanity's closest living relatives, and display impressive comprehension of physical and social relations. However, the structure of chimpanzee reasoning is controversial (Penn et al., 2008); this will be discussed in the following sections.

1.1.1.2 Social cognition and chimpanzees

In the wild, chimpanzees must be able to recognize group members after being apart for long periods; this is because of the high rate of fission-fusion within groups. When groups reunite, it is crucial for individuals to be able to recognize and

remember other group members, as opposed to non-group members. It is also essential for individuals to be able to recognize fluctuations in dominance rank among group members, which may have occurred during a period of separation. Inaccurate inference of group membership or asymmetrically hierarchical relationships could result in stressful conflict. When individuals of different groups do come into contact, violent acts of aggression often occur (Wilson et al., 2014) wherein group members gang up on non-members, and attack and sometimes kill the non-member (Goodall, 1986). Social awareness and recognition is crucial for chimpanzees, so they do not needlessly kill known, or even related individuals.

Tracking and monitoring conspecifics' interactions is also useful for primate survival (Jolly, 1966). As suggested above, chimpanzees are adept at inferring rank and relationship fluctuations from observing conspecifics' behavior (Kendal et al., 2015; Pika & Mitani, 2006; Subiaul, Vonk, Okamoto-Barth, & Barth, 2008). Chimpanzees also appear to be skilled in deception: subordinate males will mate with fertile females when the alpha or other dominant males are absent (Mitani, Watts, & Muller, 2002). This behavior suggests that the chimpanzees understand the risks of their actions and know when to take advantage of the absence of dominant individuals.

In captivity, researchers have found that chimpanzees can predict the actions of individuals based on physical signals (i.e., hair standing up, swaying, body orientation), follow the gaze of humans and conspecifics, and they can assist a human to achieve a clear goal such as obtaining an out of reach object (Barth, Reaux, & Povinelli, 2005; Hare, Call, & Tomasello, 2001; Warneken & Tomasello, 2006)

Gaze following is of particular note, as it allows individuals to extract information from one another. This information may concern social relations within the group, or activity of outsiders, including conspecifics and predators. And yet, not all chimpanzees are proficient at following gaze or gestures, so in other words, individual differences are present.

1.1.1.3 Physical cognition of chimpanzees

Problem solving, especially concerning tool-use, is of primary interest for investigators of chimpanzee physical cognition, for chimpanzees naturally use tools in the wild. Moreover, researchers have argued that tool-use reflects causal understanding of the relationship between the tool, the target, and the actions required to put tool the tool into use to obtain the target reward (Deaner, van Schaik, & Johnson, 2006; Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995). Chimpanzee tool-use, such as using a twig to extract termites from a colony mound, has been studied in the wild (Boesch & Boesch, 1990) and in captivity (Celli, Tomonaga, Udono, Teramoto, & Nagano, 2003). Goodall (1964) first observed chimpanzees using tools to feed on insects in this way, and since then, observations of this behavior have been frequent and widespread in wild populations (Boesch & Boesch, 1990; McGrew, 1974; Nishida, 1973). The materials and methods of tool-use had been found to vary among wild chimpanzee populations (McGrew, 1992) Wild chimpanzees modify sticks for use as tools, but the modification depends on the purpose of the tool. For instance, chimpanzees fashion tools from sticks of two different sizes: longer, thicker sticks used to probe for ants and honey, and smaller sticks for picking out and eating bone marrow. In almost all instances, the chimpanzees modified the sticks for the task before making any attempts to use the

stick, which suggests that chimpanzees understood the relationship between these tools and the task (Boesch & Boesch, 1990).

In captivity, the strengths and limitations of chimpanzee tool-use has been the subject of much research (Köhler, 1925; Mulcahy & Call, 2006; Murray, Lonsdorf, Eberly, & Pusey, 2009; Povinelli, 2000; Visalberghi et al., 1995). To enhance understanding of the limitations governing chimpanzees' reasoning skills regarding tool use, many researchers have used tasks wherein subjects must select the correct tool from a set of tools, some of which are functional for solving the task, and some of which are not (Povinelli, Reaux, Theall, & Giambrone, 2000; Yocom & Boysen, 2011). Other researchers have employed tasks which require that their subjects modify the tool to solve the task (Visalberghi et al., 1995).

In the early study by Visalberghi et al. (1995), chimpanzees (and other apes, and capuchins) were tested with a perspex tube containing a food reward in the centre. The researchers provided the chimpanzees with a varying selection of tools, some of which could be easily used to solve the problem, and others which required modification. The chimpanzees were able to solve both types of problems, but small individual differences in performance were present, which the researchers did not interpret. In a later variant of the test, even stronger differences in performance were apparent, but the researchers chose to focus on the number of errors that each subject made, rather than examining overall performance, which varied considerably.

1.1.1.4 Can chimpanzee intelligence be explained by a general domain?

Researchers disagree as to whether the evolution of primate cognition was driven by physical, i.e. ecological, pressures arising from the environment, or by the

social pressures of group living. Some argue for the social intelligence hypothesis (Byrne & Whiten, 1989): that the complexity of a species' intelligence depends on social effects; since group-living species are constantly engaging with social strategies and updating social information, these species are, all else being equal, more intelligent (Holekamp, Sakai, & Lundrigan, 2007; Humphrey, 1976; Jolly, 1966). This theory has come under increasing fire in recent years (DeCasien, Williams, & Higham, 2017; Holekamp, 2007). Some researchers argue that ecological pressures are equally if not more important to understanding the evolution of intelligence (Rosati, 2017). Another group of researchers argue that the evolution of cognition was driven by a general intelligence factor which encompasses the domains of both the social and physical worlds of animals (Burkart, Schubiger, & van Schaik, 2016).

Though we have defined general intelligence in humans, how to describe analogous aptitudes in primates, or other animals, is not obvious. Researchers usually define domain-general intelligence in animals as the ability to excel in a multitude of contexts and on a wide variety of cognitive tasks (Burkart et al., 2016). A species or individual that performs well consistently would provide straight-forward support for the theory of general intelligence.

Until recently, comparative research placed little focus on domain-general intelligence within species, yet some studies investigated domain-generality of intelligence across species. Deaner et al. (2006) meta-analysed 30 studies of non-social cognition in nonhuman primates, and found evidence for general intelligence, as well as significant differences in general intelligence between taxa, with hominids

outperforming all others. They aimed to restrict statistical comparisons to subjects with similar backgrounds and ages, and to tests which used similar procedures. Though the researchers were conservative and tried to compare performance only on tasks with high degrees of similarity, procedural differences were present, and perhaps most notably, tests of social cognition were excluded.

Deaner et al. (2006) argue that greater individual differences exist between species than tend to occur within species. That is, the least intelligent individual from an intelligent species will likely perform better the most intelligent of a less intelligent species. However, their meta-analysis could not comment on within-species variation in intelligence.

Herrmann et al. (2007) followed with a study of chimpanzees, orangutans, and human children, all of whom were tested with a battery of cognitive tests which assessed both their social and physical intelligence. The resultant Primate Cognition Test Battery (PCTB) was composed of three sub-categories of physical tests and three sub-categories of social tests, totalling 16 tasks. The physical tasks were chosen for their ability to investigate spatial reasoning, numerical cognition, and causality (for example, object permanence, adding numbers, and tool-use ability, respectively). The social tasks assessed theory of mind, communication, and social learning. Herrmann et al. (2007) found that apes and human children displayed similar aptitudes for the physical tests, but children outperformed apes on social tasks. The researchers argued that their results contradicted the general intelligence hypothesis because the children demonstrated advanced skill in one, but not both, of the domains tested.

Subsequent analyses of these data by Herrmann, Hernández-Lloreda, et al. (2010) found inconsistencies in the assortment of their tests under their theoretical latent variables, e.g., children's performance was best modelled with 3 factors: social, physical, and spatial, yet the chimpanzee data supported an unintuitive two-factor structure: a spatial domain, and a combined physical-social domain. Some critiques have suggested that these discrepancies in structure may be attributable to some of their measures having low reliabilities (Bouchard, 2014). On the other hand, another large study of chimpanzees that used the PCTB found clear evidence for a general intelligence factor (Hopkins et al., 2014). Similarly a recent, large and comprehensive study found a general intelligence factor in dogs (Arden & Adams, 2016). These findings join a significant body of research which has found evidence of general intelligence in species as distant as mice (Matzel et al., 2003) and robins (Shaw, Boogert, Clayton, & Burns, 2015).

Much of the recent work on chimpanzees' general cognitive ability has been studied in conjunction with other individual differences, especially personality. We will return to these studies after introducing personality.

1.1.2 Personality

1.1.2.1 Foundations in animals

Animal personality is the study of behaviors that are repeatable across time and contexts (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). The modern empirical study of personality – both human and nonhuman – began with dogs. From the behaviorist tradition, Ivan Pavlov (1908/1941) postulated a typology that was perhaps the first system for measuring personality types in animals. Pavlov's

typology mixed three properties: Force, the ability to endure stimulation; Equilibrium, the balance between the excitable and the inhibited; Mobility, an individual's flexibility in alternating between excitable and inhibited. Mixing these three properties produced four personality types, such as Lively (high Force, moderate Equilibrium, high Mobility) and Quiet (high Force, moderate Equilibrium, moderate Mobility). Pavlov always assessed these personality types as representations of different associative learning characteristics in his dogs.

After the dogs came chimpanzees. Robert Yerkes' (1939) study of primates led him to argue that personality existed among chimpanzees (*Pan troglodytes*), though he did not refer to personality types or identify specific dimensions. Yerkes and collaborators relied on scales that independent raters completed (Crawford, 1938). The ratings were consistent between raters, and particularly those raters who had more experience with that sample of chimpanzees; moreover, these personality traits could be aligned along "group factors". Groupings of variables, such as Crawford's, are now known as factors, components, or, when studied by behavioral ecologists, behavioral syndromes (Sih, Bell, Johnson, & Ziemba, 2004). In the same group of chimpanzees, Hebb (1946a) looked to emotions to describe individual differences, and used pre-specified ethograms to code behaviors, in response to a range of test conditions (Hebb, 1946b, 1949). Early observations of nonhuman primate personality were not restricted to studies of captive chimpanzees. For example, Junichiro Itani (1957) and Jane Goodall (1990) commented on and described the personalities of wild Japanese macaques and wild chimpanzees, respectively.

1.1.2.2 Development in humans

Around the same time as Yerkes and Crawford were studying chimpanzees, Allport and Odbert (1936) inspired by Francis Galton's Lexical Hypothesis (Galton, 1884), identified nearly 18,000 terms from Webster's New International Dictionary that could be used to describe personality and behavior in humans. Norman (1963) removed archaic, redundant, offensive and obsolete terms from the list, reducing it to a mere 2,797 unique terms, which could be used to describe human personality.

Efforts to use systematic descriptors derived from natural language powerfully influenced researchers in subsequent decades. Cattell, a pioneer of factor analysis, identified sixteen primary and eight secondary personality dimensions (Cattell, 1946). However, Cattell's structure was too complex for other researchers to replicate. They argued that Cattell's interpretation of the correlational structure of the data was too liberal, and fewer dimensions would better represent personality. Fiske, notably, argued that five factors were enough to describe personality (Fiske, 1949).

However, the next major step in personality research may have been a leap too far. Hans Eysenck recognized a need for reducing the abundance of constructs and theories into as few as possible. He factor analyzed personality descriptors, reducing them to basic dimensions, which he referred to as traits. Eysenck defined traits as "observed constellations of individual action-tendencies" (Eysenck, 1944), or in other words, habits or repeated behaviors that consistently group together form a trait.

Eysenck conducted his first major study with seven hundred soldiers (Eysenck, 1944). They rated themselves on thirty-nine descriptive items, and

Eysenck factor analyzed these data. His second major study vastly increased in scale; Eysenck conducted a similar analysis on almost 10,000 individuals. From these studies, Eysenck concluded that human personality was composed of two basic dimensions: Neuroticism and Extraversion.

Eysenck defined Neuroticism as the tendency to experience negative emotions and Extraversion as the tendency to enjoy positive, and in particular social, events. Eysenck also drew inspiration from Pavlov's typologies, and in later work added a third dimension, psychoticism, after extensive observations of psychiatric patients (Eysenck, 1950). Eysenck's influence on the study of individual differences in health will be discussed in more detail in section 1.2.

Researchers have debated whether three or more personality dimensions are the best model for human behavioral differences, and ultimately Eysenck's three dimensional model has failed to overcome recent empirical challenges (Costa & McCrae, 1992a, 1992b). Instead, the Five-Factor Model (FFM) emerged as the dominant model of personality in modern psychological science.

First suggested by McDougall (1932), and later (Fiske, 1949), these factors were not verified until Tupes and Christal (1961) re-analyzed Cattell's personality data and found five factors similar to McDougall's factors. Yet, the FFM did not see widespread adoption because Tupes and Cristal published their findings in an obscure American military technical report. Nevertheless, over the remaining decades of the 20th century, the FFM was increasingly shown to be robust (McCrae & Costa, 1987). The FFM is also known as the "Big Five" because each factor is broad (John & Srivastava, 1999). The FFM does not suggest that five factors and five

factors alone encompass the full range of personality; rather, the five factors represent personality at its most abstract, and each factor summarizes many distinct and specific characteristics. Each factor remains partly ambiguous, in that no single label, or even collection of labels, can capture every aspect of each personality dimension (Digman, 1990). However, the name of each factor represents a center point, and these names - Neuroticism, Extraversion, Openness to experience, Agreeableness, and Conscientiousness - have become ubiquitous.

In the FFM, Neuroticism captures an individual's propensity for negative affect, which is why Neuroticism is sometimes referred to as Negative Emotionality, or just Emotionality. Extraversion describes an individual's tendencies toward active, sociable behaviors. Openness to experience (hereafter Openness) is sometimes called Intellect, and has been repeatedly associated with intelligence. In its own right, Openness is described by an individual's creativity, inquisitiveness, flexibility of thought, and receptivity to new ideas. Agreeableness encompasses altruistic nurturing, caring and supporting tendencies; an individual low in Agreeableness would be selfish, spiteful, and indifferent to others. Finally, Conscientiousness describes an individual's dependability, prudence, and willpower (Digman, 1990).

As each personality dimension is broad, each encompasses many facets (McAdams & Pals, 2006). In different species and populations, the broadness of each dimension may cover slightly different arrangements of facets (Weiss, Adams, Widdig, & Gerald, 2011). The overall center of the dimension may not differ substantially, though in some species, names have been changed to better reflect the differences in personality across species.

1.1.2.3 A refocusing on animals

Animal personality had remained largely unstudied until the 1970s. In 1971 van Hoof used principal components analysis (PCA) and found four personality dimensions in chimpanzees: Affinitive, Aggressive, Play, and Submissive. Chamove, Eysenck, and Harlow (1972) used factor analysis with a large group of rhesus macaques (*Macaca mulatta*), finding three dimensions: Affiliative, Hostile, and Fearful. Stevenson-Hinde and Zunz (1978) followed with the publication of a rating instrument for assessing rhesus macaque personality, along with results. Observer ratings were gathered; each observer rated each monkey on various traits. These observations were analyzed with PCA to identify personality dimensions that they named Confident, Excitable, and Sociable. These studies strongly suggest that primate personality traits are organized along distinct dimensions. Furthermore, knowing which dimension describes a set of traits helps ascertain the function of traits and fitness trade-offs that maintain genetic variation among traits.

The FFM was adapted for chimpanzees in the form of the Chimpanzee Personality Questionnaire (CPQ) by King and Figueredo (1997). As hypothesized, they found what appeared to be homologues of the FFM factors. They also found a sixth factor that they labeled Dominance, which accounted for the most variance. Subsequent studies of nonhuman primates that used the CPQ and its successors, notably the Hominoid Personality Questionnaire (HPQ), also found factors or components corresponding to Dominance (e.g., Konečná et al., 2008; Weiss, Inoue-Murayama, et al., 2009; Weiss, King, & Perkins, 2006). These studies have identified human-like personality dimensions in bonobos (Weiss et al., 2015), orangutans

(Weiss et al., 2006), and macaques (Weiss, Adams, Widdig, et al., 2011), among others.

1.1.3 Covariation in animal personality and intelligence

Pavlov assumed that personality could predict performance outcomes of training and testing, and defined his typology with the goals of the behaviorists in mind. By definition, personality is behavioral variability, making it a prerequisite for natural selection (Dingemanse & Réale, 2005). When one also considers that personality and cognition are linked in humans (Ackerman & Heggestad, 1997), one might expect that personality and cognition evolved in concert. Modern models of animal personality little resemble Pavlov's, and the question has yet to be answered: Is personality linked with differences in cognitive abilities?

In humans, there are multiple mechanisms whereby personality might be linked to intelligence. The clearest connection is between Openness and *g*, where as much as 40% of the true variance of Openness could be attributed to *g* (Chamorro-Premuzic & Furnham, 2014). One reason for the overlap might be due to self-report of personal cognitive ability, a subjective measure, but which is at least somewhat accurately tapped into by the questions posed by Openness inventories. Nevertheless, in factor analyses, the ability items are part of the same factor as other items relating to openness to fantasy, aesthetics, values, and feelings (McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005), suggesting that higher Openness individuals are generally more intelligent. However, the relationships between the other personality dimensions and *g* are smaller, and not strongly believed to be the result of cognitive overlap.

Meta-analyses have also linked Extraversion to intelligence, but particularly test-taking characteristics and behaviors. For example, high Extraversion individuals display better short term memory retrieval, are more resistant against distraction, and better at timed tasks, but low Extraversion individuals appears to have better long-term memory and reflective problem solving abilities (Matthews, 1999). Given this divide, estimates of a correlation between Extraversion and *g* have varied from positive to negative.

Neuroticism relates to intelligence scores in a similar fashion as Extraversion. Higher Neuroticism individuals perform more poorly under stressful test-taking conditions. Neuroticism has a negative correlation with intelligence across multiple studies (Zeidner & Matthews, 2000); the conclusion often drawn from these results is that negative affective attributes such as anxiety and worry interfere with cognitive processes, such as memory and attention, that are required to succeed on tests (Chamorro-Premuzic & Furnham, 2014).

Agreeableness appears to be the least related to cognitive ability. Although, some researchers argue that these relationships have not been sufficiently studied for this dimension (Chamorro-Premuzic & Furnham, 2014). Conscientiousness, on the other hand, may be as weakly related to cognitive ability as Agreeableness, but has major positive associations with life outcomes, such as academic and job performance (Hurtz & Donovan, 2000; Poropat, 2009), which, all else being equal, are outcomes also linked to intelligence.

However, a fundamental problem with describing relationships between personality and cognitive abilities, particularly in animals, is selection bias. Animals

that are more likely to participate in tasks tend to represent particular personality profiles (Morton, Lee, & Buchanan-Smith, 2013); other individuals may choose not to participate, or their data may be discarded for a variety of reasons (incompleteness, messiness, etc.). Even in studies where animals are subjects rather than participants, distractibility can impact performance, making it difficult to assess pure cognitive ability.

Much research has focused on the connection between exploratory behavior and task acquisition. In general, more exploratory monkeys, mice, and corvids learn more quickly (e.g., Coleman, Tully, & McMillan, 2005; Guenther, Brust, Dersen, & Trillmich, 2014; Matzel et al., 2003) and innovate more frequently (e.g., Stöwe, Bugnyar, Heinrich, & Kotrschal, 2006). In social species, an individual's connectedness and/or dominance within the group could impact the effectiveness of learning (e.g., Herrelko, Vick, & Buchanan-Smith, 2012; Stöwe et al., 2006).

As ever in animal cognition research, transfer is the gold standard cognition; compelling work would show that different personalities are repeatedly associated with performance on a variety of tasks. For example, although more conscientious individuals may acquire initial tasks faster and be rewarded more reliably, if the reward contingency changes, more open individuals might be able to adjust more effectively. Teasing apart contributions from multiple personality dimensions would allow us to understand the structure and complexity of animal intelligence, or intelligences.

1.2 Relationships between psychology and health: psychosomatic medicine

The study of animal cognition has a long and storied history, and while animal personality research did not gain traction until more recently, animal personality research has exploded in the last two decades. In contrast, the study of psychosomatic health in animals is very small. Thus, we must first turn to the rich history of behavioral medicine and psychosomatic research in human beings.

1.2.1 Origins

The role psychological factors play in the pathogenesis of somatic ailments became widely accepted during the heyday of psychoanalysis. Psychoanalytic theory was itself a response to the mechanistic medicine of the 19th century. Psychoanalysis treated the human organism as a single, functional unit; the body's functional systems, which included the mind, impacted each other in powerful, but often negative ways. Freud himself was interested in psychosomatic ailments, an interest which developed out of a correspondence with notable medical researcher Georg Groddeck (Freud, 1974).

Franz Alexander (1957), a contemporary and collaborator of Freud's, viewed personality as "…the expression of the unity of the organism. As a machine can only be understood from its function and purpose, the understanding of the synthetic unit which we call the body can only be fully understood from the point of view of the personality, the needs of which are served by all parts of the body in an intelligible coordination." (p. 34). In other words, Alexander saw perturbations of organs or systems as a consequence of the aforementioned "unity". Alexander and Dunbar thus

proposed that emotions that are not openly expressed will result in somatic illness (Alexander, 1957). Dunbar and Alexander went so far as to identify seven ailments that, according to them, had psychological origins, and called them psychosomatic diseases (Dunbar, 1947). These diseases were: asthma, hypertension, ulcerative colitis, Graves' disease, arthritis, stomach ulcers, and neurodermatitis.

The early body of research in psychosomatic medicine had many methodological issues. They often used retrospective analyses, and relied on samples of psychiatric patients. Because the studies were driven by theory alone, and possessed little empirically grounding, their findings failed to replicate, and their theories were later abandoned. But, these theories paved the way for evidence-based medicine to develop psychosomatic medicine into a fully empirical field.

1.2.2 Empirical beginnings

Friedman and Rosenman (1959) were the first to discover an association between behavioral factors and coronary heart disease. They linked these health outcomes to three 'types' of observable behavior in relation to work characteristics and performance.

Type A individuals are characterized as intense, and possessing of a need for achievement, a sense of urgency, and a strong desire to compete. Type B is the opposite of Type A, and thus refers to individuals who lack drive, ambition and competitiveness. Type C is similar to B, but adds chronic anxiety. Friedman and Rosenman compared serum cholesterol levels, clotting times, and presence of coronary heart disease in males divided into three groups defined by the A, B, and C behavioral patterns. They found that serum cholesterol levels were significantly

higher in the type A group (253 mg per 100 ml) than in either the type B (215 mg per 100 ml) or type C (210 mg per 100 ml) groups. Moreover, the Type A group displayed significantly quicker blood coagulation, and a higher incidence of coronary heart disease than either of the other groups. These differences could not be explained by differences in diet, exercise, alcohol intake, or smoking (Friedman & Rosenman, 1959).

Researchers concluded that the Type A behavioral pattern was a "coronary-prone personality" (Price & Clarke, 1978). This assertion marked the beginning of evidence based psychosomatic medicine. From here, the field was propelled towards studying personality characteristics in relation to health and particularly cardiovascular diseases (CVDs).

In many future studies, the definition of Type A behavior was expanded to include characteristics such as hostility and anger. Three decades after the Type A behavior pattern was introduced, the first quantitative review of the literature was published (Booth-Kewley & Friedman, 1987). This review included measures of anger, hostility, aggression, depression, anxiety, extraversion, and the Type A behavior pattern as predictors, and CVDs such as coronary heart disease, atherosclerosis, myocardial infarction, angina, and combinations of the preceding, as outcomes. In the 55 published reports, the Type A behavioral pattern was associated with combined heart disease outcomes. This relationship was undoubtedly significant, but the effects size was small ($r = .14$), and the component of Type A behavior - competitiveness/hard driving/aggressiveness - was most strongly related to coronary heart disease. However, other personality variables associated with

negative affect were also significantly related to CVDs, including anger, hostility, depression, and anxiety. The strongest predictor was hostility (r = .21); the combined effect size was stronger than that for Type A behavior.

Booth-Kewley and Friedman (1987) concluded that cardiovascular risk was not associated with impatient, hectic, workaholic tendencies, but by negative emotions. That is, individuals who were, to name a few examples, depressed, aggressive, anxious, or easily frustrated were at higher risk. Among these items one can see pathological descriptors, like depressed or anxious, which in part led the reviewers to posit that although this maladapted personality is one that is prone to developing CVDs, it may also increase the hazard of developing other diseases. The reviewers proposed that 'disease-prone personality' may be a causal factor in disease ontogeny (Friedman & Booth-Kewley, 1987).

This construct co-emerged from another meta-analysis conducted by the same authors, but on the literature surrounding personality correlates of five psychosomatic diseases: asthma, arthritis, ulcers, and headaches, along with aforementioned coronary heart disease. Prior literature suggested that the asthma-prone personality was anxious, dependent, aggressive, and neurotic. Headaches had been linked with stress, anger, repressed hostility, and emotional tension. Peptic ulcers were also associated with chronic exposure to stress, and rheumatoid arthritis was associated with depressed, perfectionistic, and repressed personality. Given that these diseases had been associated with (albeit a wide range of) negative affective traits, Friedman and Booth-Kewley (1987) conducted a meta-analysis to test the proposed associations between personality and disease. Personality variables were

grouped into following categories: anxiety, depression, extraversion, one combining anger and hostility, and one combining anger, hostility, and aggression. The meta-analysis included 101 published studies.

Overall, the reviewers found consistent associations between personality and diseases. However, they found no specific arthritic or coronary-prone personality, as no independent associations between any specific personality traits and any particular disease were found. The magnitude of the correlations were the same as those described for CVD, ranging between approximately .1 and .2 for specific outcomes. Taken as a whole these results supported the existence of a generic disease prone personality typified by tendencies to experience negative affect, e.g., anxiety, depression, hostility, anger, and aggressiveness (Friedman & Booth-Kewley, 1987). It was unclear what mechanism or mechanisms were underlying the associations; negative affective experiences might have been causing health issues, but negative emotions like these are often reactions to a negative life event, or the result of external stress, which could be the root cause of poor health.

Independently of Type A and disease-prone personality research, but around the same time, endocrinologist Hans Selye proposed the General Adaptation Syndrome theory of stress (Selye, 1956). If stress is defined as a sum effect of bodily processes reacting to a real or imagined stressor, the General Adaptation Syndrome model describes the body's reaction to stressors, characterized in three phases.

Phase 1 is a nonspecific mobilization phase. There are two stages within this phase. An initial shock reaction to a stressor induces physiological changes, such as decreased blood volume and levels of electrolytes and sugar in the blood. When the

stressor is identified, the body then starts to respond as to a state of emergency: the sympathetic nervous system activates, epinephrine is produced and released. This second stage of responses result in increased muscle tone, blood glucose, blood pressure, and heart rate.

Phase 2 is called the resistance phase, and is characterized by increased secretion of glucocorticoids, which augment the body's ability to cope with stressors. During this phase, glucose, fat, and protein in the blood increases, and potassium levels decrease. These effects are unsustainable, as the body's resources will deplete. Depending on the extent to which the resources are lost, the final stage of the stress response will be either exhaustion or recovery. If the body successfully copes with the stressor during the resistance phase, then a recovery phase will occur; levels of glucose, fat and protein in the blood will decrease and return to normal, restoring homeostasis.

If the body is exposed to the stressor for a prolonged period during the resistance phase and unable to eliminate the stressor, once resources are depleted, the body will be unable to maintain normal function and an exhaustion phase will occur. If an exhaustion stage is sustained for too long, tissue damage, or even death, may occur. Prolonged and/or repeated overactivation of the sympathetic nervous system and exhaustion of the immune system has been shown to result in the digestive tract disturbances, diabetes, and cardiovascular issues (Taylor & Sirois, 1995). A useful variable for measuring prolonged or repeated exposure to stress is known as allostatic load (McEwen & Stellar, 1993). Allostatic load will be discussed in greater detail in chapters 5 and 6.

Friedman and Booth-Kewley's (1987) idea of the disease-prone personality meshed well with the General Adaptation Syndrome model, rather than with the earlier psychosomatic theories of unresolved psychological conflicts offered by Alexander, Dunbar, and other advocates of the psychodynamic approach. Rather than affecting specific organs, psychological disturbances appear to impact the autonomic nervous system, immune system, and metabolic processes. Disrupting these systems can lead to any number of negative health outcomes. The General Adaptation Syndrome model suggested a biological mechanism through which excessive exposure to stress would lead to disease.

However, recognizing the presence of a particular stressor is insufficient to explain the myriad of potential negative resultant health outcomes. A range of individual differences exists in how stress is perceived, and the lasting effects of the same stressful events (Watson, 1988; Watson & Pennebaker, 1989). This variation suggests that there is a trait-like tendency within individuals, which affects how they experience and react to negative affect. Thus, researchers proposed that negative affect was a possible mediator of the associations between physiological stress and psychological variables.

1.2.3 Eysenck and biological theory

Eysenck's personality dimensions were strongly rooted in his arousal theory of personality (Claridge & Eysenck, 1967). According to the arousal theory, individual differences in Extraversion reflect individual differences in response thresholds of the ascending reticular activating system, a set of sub-cortical structure within the brain. Introverts have lower stimulation thresholds, and consequently are

more reactive to environmental stimulation of all kinds and, somewhat unintuitively, have higher baseline levels of cortical arousal. Extraverts are the opposite: they require more external stimulation to reach equivalent levels of arousal as introverts.

In the arousal theory, Neuroticism is rooted in a different set of brain structures: the limbic system. Individual differences in the activation of the limbic system could produce differing degrees of either emotional stability and instability (Claridge & Eysenck, 1967; Corr, 2004). The proposed biological link between Neuroticism and the limbic system provided an easy explanation for Neuroticism's relationship with health, namely as the limbic system was, in turn, linked to unhealthy activation in the autonomic nervous system, which is itself in turn related to cardiovascular disease (Matthews & Gilliland, 1999),

As mentioned previously, Eysenck's theories did not stand the test of time. Nevertheless, they were influential for many years, and drove a great amount of research towards the study of the biological basis for personality, particularly in relation to psychosomatic health, including some specific health outcomes, e.g., stress and cardiovascular disease.

1.2.4 Associations with health in the FFM

As previously mentioned, CVD is often related to hostility and Type A behavior; how are these association reflected by the FFM? Hostility and antagonism are most closely tied to low Agreeableness, but to a lesser extent, high Neuroticism (Deary, Weiss, & Batty, 2010; Dembroski & Costa, 1987) as well. These findings make sense, as Agreeableness and Neuroticism are the FFM traits most strongly

related to negative affect. Either trait, or both in combination, could lead to poorer health generally, as well as CVD and early mortality.

Some studies have found that Neuroticism is associated with health outcomes in people with multiple diseases, which is additional indication that Neuroticism may be tied to a general susceptibility to ill health rather than any specific disease (Matthews, Deary, & Whiteman, 2009) Neuroticism has become recognized in the field of public health as a major contributor to excess healthcare costs (Lahey, 2009), which for highly neurotic individuals are approximately 2.5 times higher than those brought on by common mental health disorders (Cuijpers et al., 2010). However, the mechanisms through which Neuroticism influences health are not fully understood. Openness has also been linked to CVD. Specifically, facets of Openness, including Openness to feelings, aesthetics, ideas, and actions have all linked to reduced risk for cardiac (Jonassaint et al., 2007) and all-cause (Ferguson & Bibby, 2011) mortality.

The Framingham Heart Study had a profound influence on large, longitudinal studies of human health. As a consequence of this foundation study, research tended to focus on cardiovascular health during the 20th century. However, more recent work has emphasized the impact of personality on other dimensions of health. Goodwin and Friedman (2006) found that Conscientiousness and Neuroticism were related to several self-reported diseases in a national representative sample. Individuals who reported having diabetes, hernia, hypertension, or bone and joint problems were lower in Conscientiousness. Individuals with ulcers, bronchitis, asthma, and other respiratory problems were higher in Neuroticism. Furthermore, individuals who reported having chronic skin conditions, urinary–bladder problems,

stroke, or tuberculosis were more likely to have both lower Conscientiousness and high Neuroticism (Goodwin & Friedman, 2006).

Personality traits have also been linked to mortality, or length of survival. Meta-analysis (Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007) showed that low Conscientiousness, Extraversion and Agreeableness, and high Neuroticism were all associated with higher risk of all-cause mortality. Conscientiousness was the strongest and most consistent predictor of survival time in this meta-analysis, while the associations between Neuroticism and survival were inconsistent. Some studies found that Neuroticism was associated with an increased, and in some cases with a reduced risk of death (Deary et al., 2010). A more recent metasynthesis that examined the FFM's relationship with mental, physical, and overall health, as well as health behaviors (Strickhouser, Zell, & Krizan, 2017) found that Agreeableness and Conscientiousness were positively, and Neuroticism negatively, associated with mental and general health, plus health behaviors. No personality dimension was consistently associated with physical health, however. Of all the FFM dimensions, Conscientiousness is the most frequently and strongly linked to mortality and health, and this has been consistently replicated across reviews and meta-analyses (Bogg & Roberts, 2004, 2013; Kern & Friedman, 2008).

Lastly, personality traits have been associated with disease precursors. High Conscientiousness and low Openness have been linked to low levels of inflammatory markers, specifically C-reactive protein and interleukin-6 (Luchetti, Barkley, Stephan, Terracciano, & Sutin, 2014). It also appears that individuals high in both

Conscientiousness and Neuroticism tend to have the lowest levels of interleukin-6 (Turiano, Mroczek, Moynihan, & Chapman, 2013).

1.2.5 Cognitive Epidemiology

Cognitive epidemiology is the study of how intelligence relates to health outcomes, including disease ontogeny and mortality (Calvin et al., 2011). The evidence to support intelligence-health associations is strong, though cognitive epidemiology as a field, despite having grown precipitously, is young compared to the field surrounding personality. The first study was by Maller (1933), who found an inverse association between childhood test scores and mortality risk. A second study followed 55 years later (O'Toole, Adena, & Jones, 1988). Finally, 13 years further on, Whalley and Deary (2001) confirmed the same negative correlation in a population representative sample, which was also subject to long-term follow up (65 years). The publication of these findings in a mainstream medical journal led to the rapid development of the new field of cognitive epidemiology. The core finding has since been replicated in many other large samples (Calvin et al., 2011).

As we have implied, large-scale studies of primate intelligence are few compared to studies of personality. As such, the studies described in this document will investigate relationships in primates between personality and intelligence, and between personality and health, but not directly between intelligence and health. Therefore, a discussion of the theory and proposed mechanisms underlying cognitive epidemiology is beyond the scope of this document.

1.2.6 Hypothesized mechanisms linking personality with health

As established, considerable, convincing evidence exists that the personality traits of the FFM are associated with CVD, mortality, and health. However, if one proposes that personality plays a pivotal role in disease development, what are the mechanisms through which personality exerts its influence? We will describe several major possibilities.

1.2.6.1 Direct Influence

Personality might causally contribute to disease onset by directly influencing a physiological mechanism that causes disease. If a personality dimension is characterized by an underlying pattern of emotional response, then an individual who rates highly on that dimension would have a corresponding physiological response, either beneficial or detrimental to health, when coping with challenges that arise from interactions with the environment. For example, higher Neuroticism individuals might react more strongly to stressful events, and their corresponding physiological responses would cause more damage to the body than in lower Neuroticism individuals. Excess damage caused by physiological stress is known to lead to a number of major ailments (Assies et al., 2014; Austin, Crack, Bozinovski, Miller, & Vlahos, 2016; Martin-Subero, Anderson, Kanchanatawan, Berk, & Maes, 2016).

If this hypothesis was true, then changing an individual's personality would change their risk for developing disease (Allen, Magee, Vella, & Laborde, 2017; Chow, Wagner, Lüdtke, Trautwein, & Roberts, 2017; Roberts et al., 2017). However, this hypothesis does not imply that personality is the only cause of a disease (Friedman & Booth-Kewley, 1987). Rather, personality is one risk factor that makes

an individual more or less prone to develop that disease. Identifying a direct influence is difficult in practice because it requires eliminating the possibility of reverse causation and third variables, discussed below.

1.2.6.2 Unhealthy behavior

Since personality dimensions incorporate broad patterns of behavior, it might be that some of these behaviors increase an individual's risk of developing a disease. For example, experiencing negative emotions might lead to binge eating, which leads to weight gain, and obesity, which significantly contributes to the development of diabetes and CVD. In this case, personality traits associated with frequent experience of negative affect, which is associated with Neuroticism, would indirectly be a source of these health conditions.

Substantial evidence has demonstrated that personality traits are related to health-related behaviors. For example, a combination of high Neuroticism, low Conscientiousness, and low Agreeableness has been linked to alcohol abuse (Malouff, Thorsteinsson, Rooke, & Schutte, 2007) and high rates of smoking (Terracciano & Costa, 2004). High Conscientiousness, high Extraversion, and low Neuroticism are associated with more physical activity (Rhodes & Smith, 2006; Wilson & Dishman, 2015), which is protective against a variety of health conditions. High Openness, high Conscientiousness, low Agreeableness, and low Neuroticism are associated with active healthcare decision making (Flynn & Smith, 2007). Mounting evidence also suggests that individuals low in Conscientiousness and high in Extraversion engage in riskier behaviors (Atherton, Robins, Rentfrow, & Lamb, 2014). Yet Friedman and Booth-Kewley (1987) observed that changes in personality will not necessarily cure a disease, unless the specific mediating behavior is affected

by the change. Thus, focusing on personality dimensions may be most useful in preventing disease from taking hold and as a tool for identifying and directing therapies to at-risk individuals.

1.2.6.3 Third Variables

A biological third variable might cause both a certain personality dimension to manifest, as well as a related disease (Friedman, 2008). There exist a wide variety of biological third variables. For example, anxiety-prone individuals tend to have higher rates of heart disease; however, if a hyper-responsive nervous system is the cause of the anxiety disorder, and the cause of the heart disease, then the hyper-responsiveness is a third variable, a physiological response that causes both the outward appearance of anxiety and the development of heart disease. The appearance of anxiety would not itself influence heart disease. Common genetic influences which shape personality traits could also serve as risk factors for a disease. In these examples, the observed associations between personality and disease are purely correlational, but this is non-obvious if researchers are not aware of the third variable.

Friedman and Booth-Kewley (1987) note that biological third variables do not preclude causal personality models. If a biological system allows for feedback to and changes in the biological variable, as a function of personality influenced physiological responding, then both could be simultaneously in play.

1.2.6.4 The body as a system

As suggested above, these theories are not mutually exclusive. It is in fact most probable that a disease will not be caused by a single factor, but will be the

result of a host of processes and feedback loops that often jointly affect health in negative ways. For example, anxiety could cause an individual to smoke more, which can in turn trigger changes in autonomic nervous activity and heart rate, which could then increase anxiety further, and contribute directly to CVD risk. For this reason, it is important not to oversimplify models.

Recently, Deary et al. (2010) suggested that the mechanisms linking personality and health outcomes can be broadly lumped into two clusters: health behaviors, and socioeconomic status (SES). They describe health behaviors as links to health outcomes as previously described (Friedman & Booth-Kewley, 1987), but their recognition of the role of SES is novel. SES is a well-known independent predictor of health outcomes (Frank, Cohen, Yen, Balfour, & Smith, 2003), and personality dimensions are also related to SES indicators, such as educational achievement and income (Deary et al., 2010; Jonassaint, Siegler, Barefoot, Edwards, & Williams, 2011). Deary et al. (2010) suggest two paths by which health behaviors and socioeconomic status could influence health outcomes: by mediating the effects of personality dimensions on health outcomes; and by modifying and moderating other risk factors, e.g., genetic predisposition. A third possibility also exists: that personality itself could moderate the existing effects of genetic risk on later health outcomes (Čukić et al., 2015)

1.2.7 Connections to nonhumans

Many primate species, notably chimpanzees and macaques, have long been used model organisms in biomedical research. These studies use animals as models for humans, to study the course of a disease, the effect of a medication, or the

physiology of the brain. Psychosomatic health in animals has received less attention in its own right (Mendoza, Capitanio, & Mason, 2000).

1.2.7.1 Subjective well-being

A large proportion of studies on animal health have examined welfare, or subjective well-being, which is one way to operationalize happiness or contentment. The study of subjective well-being originated in humans and has been studied by psychologists, sociologists, and medical practitioners (DeNeve & Cooper, 1998; Diener, Suh, & Oishi, 1997; Huebner, 1991; Lucas, Diener, & Suh, 1996).

In humans, there are at least two theoretical components to subjective well-being, one emotional, one cognitive (Huebner, 1991; Lucas et al., 1996). Perhaps the most commonly used measures of subjective well-being, the Satisfaction with Life Scale, measures three domains: satisfaction with life (a cognitive element), positive affect, and negative affect (Diener et al., 1997).

Subjective well-being has been consistently found to be associated with personality traits. Specifically, subjective well-being is known to be positively correlated with Extraversion and negatively correlated with Neuroticism, both in primary analyses (DeNeve, 1999; Diener, 1998) and meta-analyses (DeNeve & Cooper, 1998; Steel, Schmidt, & Shultz, 2008), though the magnitude of these relationships is still uncertain. Subjective well-being is also positively, but more modestly, correlated with Agreeableness, Conscientiousness, and Openness.

Subjective well-being is associated with other characteristics, too, including social relationships and genetics (Camfield, Choudhury, & Devine, 2009; Helliwell & Putnam, 2004; Weiss et al., 2016; Weiss, Bates, & Luciano, 2008), and health

(Okun, Stock, Haring, & Witter, 1984). Subjective well-being is strongly associated with self-reported positive health (DeNeve, 1999; Diener, Suh, Lucas, & Smith, 1999; Helliwell & Putnam, 2004). Lower subjective well-being is reported by individuals with poor health, but the direction of causality, or alternatively, the common exogenous variable, is not clear (Diener et al., 1999). As indicated, social characteristics, especially strong, healthy, positive social bonds, and robust social networks, are associated with higher subjective well-being (DeNeve, 1999).

Very much like personality, subjective well-being can be assessed in nonhuman primates, using observer ratings (King & Landau, 2003). Across ape species, low Neuroticism, high Agreeableness, and high Extraversion are associated with higher subjective well-being (King & Landau, 2003; Schaefer & Steklis, 2014; Weiss, Inoue-Murayama, et al., 2009; Weiss et al., 2006). Similar results have been found in rhesus macaques, with higher subjective well-being being related to high Confidence, high Friendliness, and low Anxiety (Weiss, Adams, Widdig, et al., 2011).

1.2.7.2 Mechanistic hints

Research has revealed that both personality and subjective well-being are linked to longevity in apes. Gorillas rated higher on Extraversion (Weiss, Gartner, Gold, & Stoinski, 2013) and orangutans rated as higher on well-being, live longer (Weiss, Adams, & King, 2011). It might be that more extraverted individuals benefit from socializing with others. Socialization behaviors could alleviate stress by mediating physiological stress, which could increase life span. An alternative is that Extraversion is an indicator of immune function or cardiovascular risk (Weiss et al., 2013).

Personality may influence animal health in two ways, similar to the pathways previously discussed in the context of humans. Personality could explain tendencies to engage in unhealthy behaviors, e.g., highly impulsive rhesus macaques are excessively aggressive and get into many fights (Gerald & Higley, 2002). Personality could also affect directly influence physiology, and consequently health (Capitanio, 2011). Indeed, neurobiology work points to associations between personality, physiology, and well-being (Burdina & Melikhova, 1961; Koolhaas et al., 1999; Shively et al., 2008).

Both approaches ask questions about stress and coping with stress. Some work (Koolhaas, De Boer, Coppens, & Buwalda, 2010; Sapolsky, 1982, 1990) suggests that personality and environmental factors, in concert, modulate the physiological stress response. However, the correlational nature of much of the evidence makes causal linkage ambiguous, and so does not rule out the possibility that personality and the stress response could have co-evolved, or may be genetically correlated. These possibilities would fit a model that might incorporate causal links as well as third variables, such as a hyper-responsive nervous system (see discussion above). In all cases, the role of the environment is paramount, as the social and ecological landscape produces stressors that interact with an animal's personal predilections to stress.

For additional examples, wild female baboons who tended to spend time alone had higher glucocorticoid levels, even when adjusting for dominance rank (Seyfarth, Silk, & Cheney, 2012). Personality is associated with autonomic nervous system activity in goats (Briefer, Oxley, & McElligott, 2015). Rhesus macaque

personality has been linked to immune system function in monkeys infected with simian immunodeficiency virus (Capitanio et al., 2008).

While the extent of research in nonhuman primates is limited compared to what exists in humans, overall, the results from primates reflect what has been found in humans. This suggests that the links between personality and well-being are not human-specific, but part of an ancestral link between psychology and health.

1.3 The comparative approach

1.3.1 Comparing across species and measures

Research into the similarities and differences between human and chimpanzee cognition has tended to revolve around comparisons of performance between populations and species (Boesch & Tomasello, 1998; McGrew, Tutin, & Baldwin, 1979). These studies can be informative for researchers looking to identify cognitive abilities that are evolutionarily conserved (e.g. gaze following), as opposed to abilities that are believed to be unique to humans (e.g. Theory of Mind). Nevertheless, the study of individual differences is crucial for understanding the underlying structure of human and primate cognition. Researchers have noted individual differences within species' performance, but little research has focused on the implications of these individual differences in nonhuman cognition (Thornton & Lukas, 2012). Building on the literature concerning chimpanzees, this study with chimpanzees can facilitate our understanding of the evolutionary development of the human mind and primate intelligence. An investigation of individual differences within a species has the potential to demonstrate whether reasoning in the social and physical domains are strongly correlated (i.e. relational knowledge is domain

general) or whether reasoning in these domains is compartmentalized (i.e. domain-specific). Current comparative investigations reveal contrasting results, leaving uncertainty as to the generality of primate intelligence (Deaner et al., 2006; Herrmann et al., 2007; Herrmann, Hernández-Lloreda, et al., 2010; Reader, Hager, & Laland, 2011).

Comparative researchers also tend to rely on data from few subjects as ambassadors for an entire species. For example, Project Nim (Terrace, 1987) hinged on data from a single chimpanzee to make sweeping conclusions about the hard limitations on chimpanzees' capacity for language. On the other hand, exceptional individuals such as Kanzi the bonobo, have lead researchers to speculate that bonobos are superior to chimpanzees in their ability to acquire human-like language (Savage-Rumbaugh et al., 1993). These and other small sample studies are informative for understanding specific, exceptionally trained abilities, but to understand what nonhumans tend to do, rather than what they can do, we must examine larger samples.

The expansion of inventory-based personality studies across many primate species is an excellent example of what we can learn from adequately sized comparative studies. In the case of chimpanzee personality, the six dimensional structure (King & Figueredo, 1997) has been mostly replicated (Weiss, Inoue-Murayama, et al., 2009; Weiss, King, & Hopkins, 2007) extended to bonobos (Weiss et al., 2015), and compared phylogenetically to orangutans (Weiss & King, 2015; Weiss et al., 2006), rhesus macaques (Weiss, Adams, Widdig, et al., 2011), and humans (King, Weiss, & Sisco, 2008). These comparisons not only help us to put

human personality into context, allowing us to consider how and why certain traits occur, and which traits humans share with other species, they also allow us to examine species-specific selection pressures, e.g. differences in social structure, which could contribute to the evolution and diversity of personality structure.

To understand why variance in personality dimensions exists, and how these dimensions are linked to health, evolutionary psychologists consider the ancestral environment. One possible theory is that optimal personality dimensions varied with environment (Nettle, 2006). For example, neurotic traits, which evoke vigilant and wary behaviors, could be beneficial in hazardous environments, where caution is rewarded with survival. Nevertheless, the same neurotic traits might be maladaptive in environments where there are few risks (Nettle, 2006). This theory suggests that differences in localised selection pressures have maintained heterogeneity across personality dimensions in humans.

However, other theories could account for sources of environmental variation in alternative ways. For example, selective migration and settler effects may cause local differences, within populations, in trait expression (Rentfrow, Gosling, & Potter, 2008). Additionally, trait variation could result from cost-benefit trade-offs, e.g., an extravert who takes multiple sexual partners is likely to increase the number of their offspring, relative to the average, but having more offspring brings potential costs for individual offspring survival (Nettle, 2007). Thus, understanding the costs and benefits related to particular traits could improve our understanding of how personality seems to be so intrinsically linked to cognitive capacities, health, and well-being. Research with nonhuman animals could also benefit from our

understanding not only of the origins of personality, but also of their roles of different dimensions in individual fitness.

1.3.2 The present study

This document describes several studies which have aimed to elucidate the ancestral relationships between personality and two major individual differences: cognitive ability and health. Given that a rich literature exists among these variables in humans, we wished to evaluate these associations in a close relative of humans, chimpanzees, and orient our findings in an evolutionary context.

Chapters 2 and 3 address personality and cognitive ability. Chapter 2 describes three studies with a group of 19 zoo-housed chimpanzees who interacted with touchscreen tasks over the course of 3 years of research. We found that high Conscientious chimpanzees were more likely to stick with the tasks, and performed better as a result, but once their extra experience was taken into account, their performance advantage disappeared. However, we also found associations between interest and performance with high Openness, high Extraversion, and low Agreeableness. Having established these associations in chimpanzees, with Chapter 3 we extend our inquiry to a more distant common relative of humans and chimpanzees: rhesus macaques. We examined serial cognitive ability in conjunction with personality, with 9 rhesus macaques. The macaques also engaged with touchscreen tasks, but were expert subjects and displayed plateau performance. Nonetheless we found consistent associations between many measures of performance and both high Openness and high Friendliness (which is similar to Extraversion).

In chapters 4 through 6, we transition to our studies of personality and health. Chapter 4 examines personality and longevity in a sample of 538 personality rated, captive chimpanzees. These chimpanzees were followed for between 6 and 23 years after being rated. We found that high Agreeableness was associated with longer life, but no other personality traits had a significant impact on longevity. In Chapter 5, we compared biomarkers from samples of 177 chimpanzees housed at the Yerkes National Primate Research Centre, and 29,314 humans from wave 3 of the National Health and Nutrition Examination Survey. Both samples had been tested for the most common haematological and metabolic blood biomarkers, and we used these to assess stress in the form of allostatic load, between species. We found a similar structure of biomarkers in across humans and chimpanzees. In Chapter 6, we took our allostatic load measure from chapter 5 and looked at how it was associated with personality, in the same chimpanzee sample from the Yerkes Primate Centre, and in the longitudinal Midlife in the United States and Midlife in Japan biomarker study samples, which consisted of 993 and 382 individuals, respectively. We found that Agreeableness was associated with allostatic load in both human samples, but Dominance was associated with allostatic load in chimpanzees.

Finally, Chapter 7 summarises the results presented in these empirical chapters, and places our findings in the context of the literature. We discuss the limitations of the research, and offer suggestions for future study.

2 Personality, motivation, and performance on touchscreen tasks in zoo-housed chimpanzees

2.1 The synchronous study of personality and cognition

This thesis builds on a foundation of comparative psychology of cognition and personality to a considerably greater extent than it relies on the related literature in behavioral ecology, but the two disciplines ought to be viewed as complementary approaches. Given this, we will briefly discuss the collective relevance of the behavioral ecology and comparative psychology literature, which will serve to introduce chapters 2 and 3, as both these studies contribute directly to our understanding of covariation of cognition and personality in primates.

A wide range of species show consistent, within-species individual differences in behavior. Particular sets of individual behaviors can be clustered together amongst broad dimensions, which we call personality dimensions (Weinstein, Capitanio, & Gosling, 2008). This body of research has grown rapidly in the field of animal behavior. Specific cognitive capacities are well studied in some species and on some tasks, however, consistent, within-species individual differences in cognition are comparatively understudied (Griffin, Guillette, & Healy, 2015).

Why are researchers interested in studying animal personality and animal cognition in conjunction? For cognitive researchers, a question of special importance

is whether an understanding of personality dimensions and the biological correlates of personality (Koolhaas et al., 2010) is relevant for understanding cognition (Carere & Locurto, 2011). For personality researchers, especially behavioral ecologists interested in the proximate bases and evolutionary origins of personality dimensions, the specific extent of covariation between cognitive abilities and individual personalities (Sih et al., 2004) is a matter of significant uncertainty.

A major issue with researchers' inquiries is that consistent relationships between personality dimensions and cognitive abilities are rare to find across species. For relevant examples in primate research, Morton, Lee, and Buchanan-Smith (2013) found high Openness capuchins to be better learners on one associative learning task, but not a second. Similarly, Hopper et al. (2013) studied chimpanzees exposed to two different types of foraging puzzle boxes, and also found associations between Openness and success on the first type of box, but not the second. What are we to make of inconsistent associations? Whether in birds (Guillette, Reddon, Hurd, & Sturdy, 2009), rodents (Guenther et al., 2014; Matzel et al., 2003) or primates (Herrmann, Hare, et al., 2010; Massen, Antonides, Arnold, Bionda, & Koski, 2013), studies of personality and cognition are inherently correlational, capturing the associations between a limited number of tests, usually among small samples.

Another important issue with prior studies is sampling bias (Biro & Dingemanse, 2009). As discussed in chapter 1, these biases can have a powerful influence on the associations which researchers may observe between personality and ability (Morton, Lee, & Buchanan-Smith, 2013). Individuals who are more persistent may perform better on a task, but it is difficult to determine if these

individuals are innately more intelligent, or if persistence leads to greater experience, which could confer benefits to performance. Few studies have been designed which give insight into these mechanisms.

In a review of the nonhuman primate personality literature, (Freeman and Gosling (2010), personality dimensions reflecting persistence, or Conscientiousness, were some of the least reliable, least identified dimensions in the literature. Whether or not Conscientiousness is a valid dimension of personality in animals is beyond the scope of this document, but a recent review (Delgado & Sulloway, 2017) suggests that many aspects of Conscientiousness are in fact present in birds and mammals.

Chapter 2 utilizes the HPQ, which attempts to capture the full range of behavioral variation among nonhuman primate (Weiss, Inoue-Murayama, et al., 2009). Compared to a similar questionnaire instrument which was designed from the bottom-up, the HPQ produces more reliable, distinct dimensions of personality (Freeman et al., 2013), which are not anthropomorphic projections (Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012). With an existing, validated structure of chimpanzee personality, we aimed to investigate how cognitive abilities covaried with personality, with emphasis on several understudied elements. Thus, a major aim of this study was to investigate, and possibly replicate, the associations between cognitive abilities and the six personality dimensions of the HPQ.

While the chimpanzee personality dimensions generated by the HPQ includes Conscientiousness, as mentioned above, the other five dimensions all align with some of the most common personality dimensions identified among primates by Freeman and Gosling (2010). Dominance and Agreeableness were found in 20 and

14 other primate studies, respectively. Extraversion is most similar to Freeman and Gosling's Sociability dimension, which is the most commonly identified personality dimensions, found in 69 studies. Chimpanzee Neuroticism overlaps most clearly with Freeman and Gosling's Excitability, which was found in 32 studies. And Openness, which is arguably most similar to Freeman and Gosling's Curiosity, was found in 37 studies. Thus, the dimensions of the HPQ generally align clearly with well-established dimensions of primate personality.

Another principle aim was to track chimpanzees' performance on a variety of tasks over time, making this a longitudinal study of chimpanzee cognition. Using touchscreen apparatuses and in a controlled zoo environment large volumes of high quality data were produced, contributing crucial statistical power.

A third aim was to vary the tasks systematically, with respect to both difficulty and the cognitive faculties that were tested. The degree to which we succeeded in these aims is described in the following published paper, and in the discussion afterwards. Several additional predictions which follow from these aims are described in the paper as well.

In three studies, we assessed different aspects of cognitive ability and motivation in chimpanzees housed at the Edinburgh Zoo, and related these individual differences to personality. In study 1, we used a 2-alternative forced choice paradigm to test participants' flexibility and proficiency with arbitrary associative and feature-based matching rules. In study 2, we used a delayed match-to-sample paradigm to test participants' performance on a more difficult task. In study 3, we tested whether

participants' behavior and interest changed when rewards were no longer given out by the touchscreen apparatus.

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Chimpanzee intellect: personality, performance and motivation with touchscreen tasks

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Human intellect is characterized by intercorrelated psychological domains, including intelligence, academic performance and personality. Higher openness is associated with higher intelligence and better academic performance, yet high performance among individuals is itself attributable to intelligence, not openness. High conscientiousness individuals, although not necessarily more intelligent, are better performers. Work with other species is not as extensive, yet animals display similar relationships between exploration- and persistence-related personality traits and performance on cognitive tasks. However, previous studies linking cognition and personality have not tracked learning, performance and dropout over time—three crucial elements of cognitive performance. We conducted three participatory experiments with touchscreen cognitive tasks among 19 zoo-housed chimpanzees, whose personalities were assessed 3 years prior to the study. Performance and participation were recorded across experiments. High conscientiousness chimpanzees participated more, dropped out less and performed better, but their performance could be explained by their experience with the task. High openness chimpanzees tended to be more interested, perform better and continue to participate when not rewarded with food. Our results demonstrate that chimpanzees, like humans, possess broad intellectual capacities that are affected by their personalities.

1. Introduction

Intellect is highly valued among human societies, and believed to be responsible for advances in all fields of arts and sciences [1]. Intellectual individuals are characterized as intelligent, creative, perceptive, curious, competent, quick to grasp new concepts [2] and strong academic performers [3].

These constituents of human intellect are captured by personality traits [4]. In particular, the Openness and Conscientiousness domains of the human Five-Factor Model [5] are associated with higher achievement [3]; in combination, high scores on these two domains characterize 'good students' [5]. The association between Conscientiousness and achievement stems from the fact that individuals high in Conscientiousness possess greater will and motivation to perform, whether it is in the workplace or classroom, despite not necessarily having higher cognitive ability. The association between Openness and achievement is partly explained by the former's moderate correlation with general intelligence ($r = 0.33$) [4].

Openness also overlaps with curiosity [6], need for cognition (individual attraction to tasks that require thinking) [7] and typical intellectual engagement (a mixed construct of personality and intelligence) [8]. These constructs are intercorrelated, and while they are not the same thing as cognitive ability, they are all associated with it [9].

Non-human animal personality, in addition to describing behavioural traits, is associated with cognitive ability [10]. Mice have a general learning ability that is related to exploratory tendencies [11]. Slow-exploring chickadees are more accurate on an instrumental discrimination task, but no quicker to acquire the initial task than fast-explorers [12]. Chimpanzees who explored novel features of and objects in their environment also tended to obtain more rewards from puzzles than less exploratory individuals [13]. Assertive capuchins [14] and friendly macaques [15] were more successful with cognitive tasks, compared with less assertive or friendly conspecifics.

Overall, evidence for an association between personality and cognitive ability in animals has accumulated. Extensive work in great apes, particular chimpanzees, demonstrates that performance can depend on an individual's development, specifically, their experiential history with cognitive tasks [16]. However, researchers lack an analogue for human academic performance. In other species, 'achievement' is measured primarily in terms of reproductive fitness, not grade-point average or job performance. Nevertheless, the rudiments of the 'good student' are present: chimpanzees that spend more time with puzzles and persist at tool manipulation have greater success in receiving rewards than less persistent individuals [13]. While it is not clear whether the human desire to achieve can be equated with an animal's drive to receive food rewards, animals do possess an intrinsic need for exploration [17]. Clarifying these relationships between personality and performance requires a paradigm in which any individual animal can participate in and depart from the experiment at any time. Learning and dropout among freely participating animals must be tracked and evaluated alongside personality.

Personality traits like those of humans have been found in other primate species [18]. Some of these traits describe individual differences in interest and engagement, but associations with performance on cognitive tasks have been weak. Chimpanzees' interest in a touchscreen task was associated with Openness [19], as was interest in puzzle box tasks [20]. Capuchin monkey participation in two spatial cognition tasks was correlated with Openness, but while performance on the first task was also correlated with Openness, performance on both was negatively correlated with Assertiveness [14]. Rhesus macaques' accuracy on a serial cognition touchscreen task has been associated with Openness and Friendliness [15], but that study could not report on participation. Participation in cognitive tasks appears to be biased by personality [14] and may confound results, e.g. individuals with exploratory tendencies may spend more time around and manipulating an experimental apparatus [13], which may enhance learning simply because these individuals spend more time with the task, rather than because they exhibit greater cognitive ability.

Overall, these earlier findings suggest that intellect's relationship with personality has deep evolutionary roots. To test whether this was the case, we conducted three studies using touchscreen tasks among 19 zoo-housed chimpanzees to determine the degree to which chimpanzee personality domains, particularly Conscientiousness and Openness, are related to engagement and cognitive ability. Personality was measured independently in 2010, 3 years before these studies began. Intellectual engagement was tracked by amount of participation in the tasks; cognitive ability was measured via standard performance metrics for touchscreen tasks: accuracy and response time (RT).

We advance five predictions. First, we expect to replicate previous associations between Openness and greater participation. Second, we would expect individuals (rated as being) high in Conscientiousness to (i) participate for longer periods of time and (ii) show fewer dropouts. Third, we expect that if experience

on the cognitive tasks drives the relationships between personality and performance, then the effects of any personality factor would be reduced by controlling for experience on these tasks. Fourth, if performance is not driven by experience, then we would expect that, like in humans, Openness would be associated with better performance. Fifth, we predict that in conditions where food reinforcers are not provided by the task, individuals higher in Openness will still participate.

2. Study 1

2.1. Methods

Unless otherwise indicated, methods were the same across studies. Participants were a socially housed group of 19 chimpanzees (11 females, 8 males; between 14 and 50 years of age) at the Royal Zoological Society of Scotland's (RZSS) Budongo Trail exhibit at the Edinburgh Zoo. During RZSS pre-specified research blocks, the full group was given simultaneous access to a computer touchscreen set-up in the off-show bedding area of the enclosure. During research times, individuals were free to approach and engage with the apparatus, and could stop participating at any time. Individuals were limited in the number of trials they could complete per day before they were no longer allowed to participate for the rest of that day. Although there were a few cases of individuals stealing rewards from others, this behaviour was rare, and the majority of the time, the chimpanzees took turns interacting with the apparatus without conflict.

Personality was assessed prior to this research, as part of an earlier study [19] by independent researchers and raters. Chimpanzees were rated using the Hominoid Personality Questionnaire (HPQ) [21][1] by keepers and researchers who were working at the Budongo Trail exhibit at the time. Chimpanzees were rated by two or three independent raters, all of whom had at least two years of experience with the individuals they rated. The electronic supplementary materials provide full details on personalities, apparatus and enclosure.

Chimpanzees were trained and tested using a two-alternative forced choice task [22]. Participants had to choose one of two visual stimuli presented on the touch-sensitive screen, which required the use of a feature-based or arbitrary associative rule. Each stimulus was composed of a series of square framed, abstract geometrical shapes. Depending on the phase of the study, between two and seven such shapes would be linearly concatenated to form each stimulus. With a few exceptions, the salient shapes of each stimulus were the first and last shapes in each concatenation. All stimuli were procedurally generated and trial unique. During the training phases, all shapes were black, while colour was added for the testing phase.

Participants were randomly selected into one of two groups. Chimpanzees in the first group learned feature-based rules; correct discriminations required that the animal choose the concatenation with the same shaped images at the ends of each concatenation, while ignoring distracting discrepancies, e.g. the colour of different shapes, the length of the concatenations or the incorporation of novel shapes. In the final test, these individuals had to transfer to a new dimension for matching: shape ceased to be salient and the correct choice became the stimulus with matching colours for the last two shapes of the concatenation. Chimpanzees in the second group learned associative rules. Having first learned to associate five pairs of shapes, these chimpanzees also needed to choose the stimulus with the first shape of a pair in the first position of the concatenation, and the second of the pair in the last position, while ignoring distractions such as mismatched colour, incorrect positioning or inverted pairs.

Each training or testing session consisted of 12 trials, and within one daily research block, an individual could engage in up to four sessions. During training sessions, if a chimpanzee chose the correct stimulus, they received acoustic reinforcement, a 'clicker' sound familiar to the chimpanzees from husbandry training, and a food reward, then the task would advance to the next trial. Food rewards varied depending on the preferences of the individuals and availability during any given day, but rewards were chosen so as to provide maximal incentive to the chimpanzee using the apparatus. If the chimpanzee chose incorrectly, an unappealing, irregular series of sounds was played, and a time-out penalty screen was displayed for 3 s. The same trial would then be repeated until the individual chose the correct stimulus.

To proceed[1] to the next stage of training, an individual had to correctly complete 33 of 48 consecutive trials. When an individual reached the testing phase, half of the trials would be stimuli pairings from earlier training stages, and the other half would be novel stimuli pairings: test stimuli that were neither

[1]The HPQ is available online at http://extras.springer.com/2011/978-1-4614-0175-9/weiss_chimpanzee_personality.pdf.

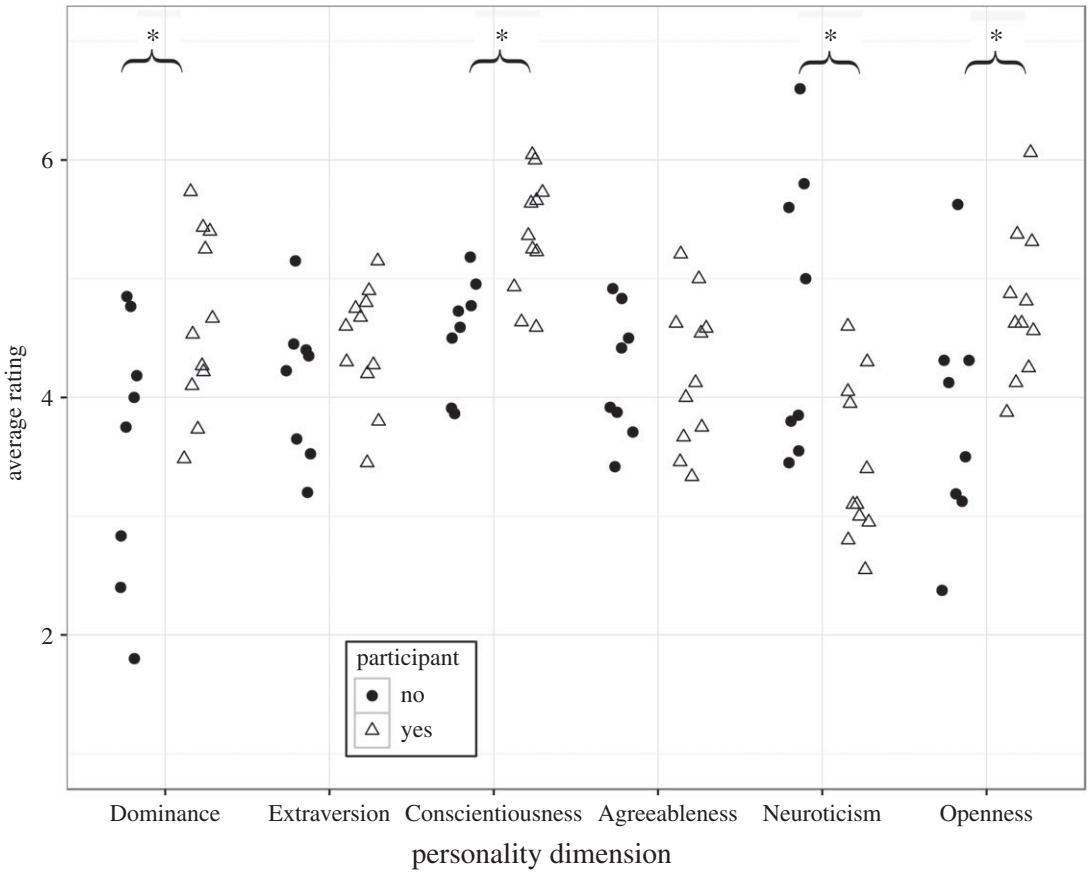

Figure 1. Filled black circles represent non-participants, hollow triangles represent participants. Non-participants did not engage with the tasks at all, while participants did to varying degrees; an analysis of dropout among these individuals can be found in table 1. Asterisks represent statistically significant differences between the groups.

fed back nor rewarded. Depending on which of two experimental groups the individuals were assigned to, the chimpanzees would have access to at most seven or 10 different tests within the testing phase. Each test consisted of a fixed number of trials—between 30 and 60. Although chimpanzees were encouraged to continue working through training and testing, they could stop participating at any time during the experiments (see Sonnweber *et al*. [22] for full details of all experimental conditions and stimuli).

2.2. Results

To assess differences in participation, we first compared the personalities of 11 individuals who participated and eight individuals who did not participate (figure 1). To be considered a participant, a chimpanzee must have completed at least a session worth of trials in one sitting. The difference between participants and non-participants was clear, as the chimpanzees who did participate all completed between 224 and 3829 trials.

Participating individuals were (rated as being) higher in Dominance ($t = 2.31$, d.f. $= 11.44$, $d = 1.14$, $p = 0.04$), Conscientiousness ($t = 3.61$, d.f. $= 15.84$, $d = 1.67$, $p = 0.002$) and Openness ($t = 2.39$, d.f. $= 10.98$, $d = 1.19$, $p = 0.04$), and lower in Neuroticism ($t = -2.69$, d.f. $= 10.22$, $d = 1.36$, $p = 0.02$). These differences survived Benjamini–Hochberg correction for multiple tests.

Of the 11 participating chimpanzees, individuals showed differing amounts of participation. Some chimpanzees stayed with the tasks longer than others, e.g. six chimpanzees progressed to the testing phase and only three completed testing. To examine the effect of personality on dropout over the course of training and testing, we fitted a Cox proportional hazards regression model with Gaussian frailty effects to the training and testing data (table 1). Chimpanzees higher in Conscientiousness were 16 times less likely to drop out; chimpanzees higher in Agreeableness were nine times more likely to drop out.

We then modelled associations between personality and learning speed using another Cox model to predict the total number of stages completed and a Poisson mixed model to predict the number of trials

Table 1. Regression analyses from Study 1. Bold text indicates significant variables, where confidence intervals do not overlap with 0.

	dropout from study		accuracy	
parameter	β	95% CI	β	95% CI
Dominance	1.12	[−1.38, 3.62]	−0.15	[−0.48, 0.15]
Conscientiousness	**−2.80**	**[−4.50, −1.11]**	0.25	[−0.45, 0.52]
Openness	−0.98	[−2.47, 0.50]	0.13	[−0.03, 0.41]
Neuroticism	1.66	[−0.98, 4.29]	0.04	[−0.34, 0.42]
Agreeableness	**2.21**	**[0.83, 3.59]**	−0.06	[−0.29, 0.18]
Extraversion	−1.00	[−2.21, 0.21]	**0.22**	**[0.01, 0.43]**
Date	—	—	**0.30**	**[0.22, 0.38]**

it took to reach criterion during training stages (electronic supplementary material, table S3). None of the personality predictors were consistently related to learning speed.

Accuracy across the task was generally good ($M = 61\%$). Although individuals displayed overall accuracy as high as 69%, two participants did not perform above chance (the lowest average accuracy was 46%). Accuracy across the training and testing stages was analysed with generalized linear mixed models (GLMM). When personality alone was used to predict trial accuracy, Extraversion and Conscientiousness were positively associated with accuracy. However, when date (representing experience with the task) was added as a predictor, only Extraversion remained significant (table 1).

RTs in all studies were calculated as the time difference between stimulus onset and the chimpanzee's first touch response to the screen, which initiated a visual and sometimes auditory stimulus change. GLMMs of RTs per trial revealed associations between faster RTs and higher Conscientiousness ($\beta = -0.53$, 95% CI [−0.92, −0.14]), Openness ($\beta = -0.38$, 95% CI [−0.76, −0.01]) and Extraversion ($\beta = -0.39$, 95% CI [−0.67, −0.10]) (electronic supplementary material, table S5). Chimpanzees can be sloppy performers, on a trial-by-trial basis, and so we tracked how many touches to the screen it took for an individual to select its intended target. A GLMM of the number of touches per trial indicated that higher Conscientiousness ($\beta = -0.38$, 95% CI [−0.76, −0.00]) was associated with fewer touches (electronic supplementary material, table S6).

3. Study 2

3.1. Methods

The chimpanzees had free access to the experimental apparatus in the research areas, or pods, of the enclosure. Unlike the bedding area where Study 1 was conducted, the research pods were viewable to the public. Otherwise, the procedure was very similar; during research times, individuals were free to approach and engage with the apparatus, and could stop participating at any time. After completing a pre-specified number of trials, an individual would no longer be allowed to participate in the task.

Study 2 used a delayed match-to-sample (DMTS) task (electronic supplementary material, figure S1): participants were shown a start stimulus which had to be touched to continue, after a 0.5 s delay a sample image was displayed in a randomly assigned location on a 3×3 grid. The sample also needed to be touched, and after another 0.5 s delay, two images, the sample, which again had to be chosen, and a distractor, were presented on the 3×3 grid. All samples and distractors were selected randomly from a large bank of colour photographic images. If a chimpanzee chose correctly, they received acoustic reinforcement and a food reward. If the chimpanzee chose incorrectly, an unappealing acoustic signal was played, and a time-out penalty screen was displayed for 2 s. After correct and incorrect trials, there was a 0.5 s intertrial interval, and no repetition of trials, i.e. no correction procedure was used to amend incorrect responses by the chimpanzees.

We also collected ordinal data on the chimpanzees' daily engagement in the research areas. Every day, individuals were each assigned to one of three escalating levels: 0—the individual did not enter the research area or did not show any interest in the touchscreen, 1—the individual showed interest in and approached the touchscreen, but did not complete any trials and 2—the individual interacted with the touchscreen and completed as least one trial.

Table 2. Regression analyses from Study 2. Bold text indicates significant variables, where confidence intervals do not overlap with 0.

	engagement		accuracy	
parameter	β	95% CI	β	95% CI
Dominance	−0.71	[−1.74, 0.33]	0.20	[−0.07, 0.47]
Conscientiousness	0.34	[−0.71, 1.40]	0.09	[−0.14, 0.32]
Openness	**0.77**	**[0.19, 1.36]**	**0.22**	**[0.01, 0.43]**
Neuroticism	−0.73	[−1.71, 0.25]	0.00	[−0.21, 0.21]
Agreeableness	**−1.11**	**[−2.00, −0.22]**	−0.10	[−0.33, 0.13]
Extraversion	0.43	[−0.51, 1.37]	0.01	[−0.16, 0.18]
Location	**−1.27**	**[−1.76, −0.82]**	—	—

3.2. Results

Engagement data were analysed with cumulative link mixed models (CLMM). These models indicated that high Openness and low Agreeableness were associated with increased engagement with the DMTS task (table 2).

The DMTS task was slightly more difficult for the chimpanzees then the two-choice forced alternative task in Study 1. Individuals displayed overall accuracy as high as 67%, but again two participants did not perform above chance (the lowest average accuracy was 49%; $M = 54\%$). The association between personality traits and performance was modelled with GLMMs, using the same approach as in Study 1. Accuracy on the DMTS task was only associated with higher Openness (table 2). Date was omitted from the final model because including it did not improve model fit ($\chi^2 = 1.60$, d.f. = 1, $p = 0.21$). Analyses of RTs revealed consistent associations (electronic supplementary material, table S8) between faster responses, to the choice stimulus and at the test screen, and higher Extraversion ($\beta = -0.34$, 95% CI [−0.63, −0.05]; $\beta = -0.39$, 95% CI [−0.55, −0.23]). Quicker RTs at the test screen were also associated with lower Dominance ($\beta = 0.49$, 95% CI [0.24, 0.74]), higher Neuroticism ($\beta = -0.48$, 95% CI [−0.77, −0.20]) and higher Agreeableness ($\beta = -0.25$, 95% CI [−0.44, −0.06]), though the power to detect Agreeableness in this instance was quite low (26%), suggesting that this result is a false positive.

4. Study 3

4.1. Methods

Study 3 was divided into six phases. First, participants were trained on a new touchscreen task, which consisted of three horizontal bar buttons, which could appear in three positions (electronic supplementary material, figure S4). The buttons were defined by their pattern and the musical sounds they played when pressed. The positions of the buttons were randomized on each trial, though every position was filled and not every button appeared on every trial. The chimpanzees were introduced to every button individually and then in combination with all others over the course of the first four phases. In the fifth phase, the layout was changed to a 3×3 grid (electronic supplementary material, figure S5) similar to Study 2. During training, pressing any button would result in the participant being rewarded with a piece of grape, so there were no wrong answers. The only criterion to advance was that individuals needed to complete 10 trials of phases 1 through 4, and 40 trials of phase 5.

The sixth phase represented a shift in procedure. After training the chimpanzees for 12 days on phases 1 through 5, training rewards were removed, and the chimpanzees were allowed to interact with the apparatus. After all of the trained chimpanzees experienced the unrewarded version of the task, 11 days of testing began. Each day the pods were baited with pellets and straw, and the experimental programme was made available. The experimental programme did not differ from previous phases: a 3×3 of grid of buttons was displayed, sound would be played when a chimpanzee pressed a button, the screen would be randomly redrawn with the button in different locations, and no rewards were given out by the apparatus.

We monitored the time chimpanzees spent in the pods and engaged with the screen. As in Study 2, chimpanzees were free to engage with the same apparatus in the indoor research pods at any point

Table 3. Regression analyses of engagement data from Study 3. Bold text indicates significant variables, where confidence intervals do not overlap with 0.

	time spent in pods		approaches to screen		time spent at screen	
parameter	β	95% CI	β	95% CI	β	95% CI
Dominance	−0.14	[−1.60, 1.31]	−0.19	[−1.67, 1.15]	0.26	[−0.20, 0.73]
Conscientiousness	−0.25	[−1.13, 0.63]	**1.09**	**[0.15, 2.16]**	0.21	[−0.17, 0.59]
Openness	−0.06	[−0.79, 0.66]	0.46	[−0.43, 1.46]	**0.52**	**[0.21, 0.83]**
Neuroticism	−0.61	[−2.08, 0.85]	0.10	[−1.43, 1.48]	0.41	[−0.10, 0.91]
Agreeableness	−0.28	[−0.96, 0.42]	**−0.93**	**[−1.63, −0.28]**	0.19	[−0.04, 0.43]
Extraversion	**0.78**	**[0.06, 1.51]**	0.69	[−0.19, 1.70]	**−0.36**	**[−0.66, −0.05]**

during the research times, during all phases. All chimpanzees could participate, regardless of whether they had previously participated, and how many phases they might have completed.

4.2. Results

Seven chimpanzees participated in the five training phases. The differences in personality between the chimpanzees who did and did not complete training are shown in electronic supplementary material, figure S5. Tests of Conscientiousness ($t = 2.285$, $d = 1.05$, $p = 0.04$), Neuroticism ($t = -1.487$, $d = -0.73$, $p = 0.16$) and Openness ($t = 2.295$, $d = 1.11$, $p = 0.04$) revealed that the trained group was higher in Conscientiousness and Openness, but the results were not significant after Benjamini–Hochberg correction.

The results of our analyses of engagement are shown in table 3. We first regressed personality onto the amount of time that each chimpanzee spent in the pods over the course of every research block. A negative binomial GLMM indicated that chimpanzees rated higher in Extraversion spent more time in the pods ($\beta = 0.78$, 95% CI [0.06, 1.51]) during these blocks. All chimpanzees spent a majority of their time foraging for pellets, collecting straw and grooming, so to assess their interest in the touchscreen we regressed personality onto the number of approaches to the touchscreen, again using a negative binomial model. Chimpanzees higher in Conscientiousness ($\beta = 1.09$, 95% CI [0.15, 2.16]) and lower in Agreeableness ($\beta = -0.93$, 95% CI [−1.63, −0.28]) made more approaches to the screen. Finally, we regressed personality onto the amount of time the chimpanzees spent physically engaged with the screen using a Poisson GLMM. Chimpanzees higher in Openness ($\beta = 0.52$, 95% CI [0.21, 0.83]) and lower in Extraversion ($\beta = -0.36$, 95% CI [−0.66, −0.05]) spent more time engaged with the screen, despite not being rewarded with food.

5. Power analyses

Where appropriate and feasible, we carried out power analysis simulations on our reported regression models to determine the power of the significant effects of personality that we found. The results of these analyses are shown in table 4. Mean power is reported instead of median power because the mean was more conservative. The mean power of all our results fell between 67% and 89%, indicating adequate to good power [23].

6. Discussion

These studies suggest that chimpanzees, like humans, possess intellectual capacities (e.g. engagement, curiosity) and non-intellectual capacities (e.g. reward seeking, precision in touch responses) that are tied to different aspects of personality and performance. Chimpanzees higher in Conscientiousness were more likely to participate; however, when rewards were removed they abandoned the task. These chimpanzees would frequently approach the apparatus, presumably to check if rewards had been reinstated, but in spite of this, they did not spend more time in front of the screen than individuals lower in Conscientiousness. Chimpanzees higher in Conscientiousness were also less likely to drop out, but when we controlled for the effects of training, Conscientiousness did not predict accuracy.

Table 4. Power analyses for regression models across studies (*n*, number of significant effects for which power could be calculated).

parameter	mean power	range	*n*
Dominance	0.79	0.63–0.95	4
Conscientiousness	0.83	0.65–0.93	7
Openness	0.76	0.50–0.96	4
Neuroticism	0.77	—	1
Agreeableness	0.67	0.26–0.95	4
Extraversion	0.89	0.81–0.97	10

The positive relationship between accuracy and Conscientiousness was the only association we found that was eliminated by controlling for training, suggesting that high Conscientiousness chimpanzees, much like high Conscientiousness humans [3], are not inherently smarter, but achieve high levels of performance through greater expertise.

Agreeableness was consistently associated with lower participation rates and higher dropout rates. Low Agreeableness, probably less altruistic [21], chimpanzees were often inclined to spend time interacting with the touchscreen, monopolizing rewards from the task, and preventing others from participating.

While several models indicated that high Extraversion was associated with higher accuracy and higher participation, these findings were largely inconsistent; for example, chimpanzees rated higher in Extraversion showed significantly less interest in the task in Study 3. This inconsistency in associations between Extraversion and engagement is reminiscent of findings in humans [24]; Extraversion is modestly correlated with intelligence ($r = 0.08$), but not associated with academic performance. On the other hand, high Extraversion was consistently associated with faster RTs, which is consistent with the view that differences in Extraversion are underlain by differences in motor mechanisms [25].

Neither Dominance nor Neuroticism displayed any major or consistent contributions to performance or participation. This is surprising considering the importance of social hierarchy to chimpanzee behaviour [26]. Earlier evidence in other species, notably macaques, suggested that rank characteristics affected individual rhesus macaques' expression of what they learned, but only in mixed social contexts [27]. However, more recent work found that low rank predicted higher training success in long-tailed macaques, but this effect was not as influential as that of personality dimensions that were not significantly correlated with rank [28]. There is thus little evidence for a consistent relationship between Dominance or similar personality dimensions (e.g. Confidence or Assertiveness) and non-social cognition.

Previous research with these chimpanzees showed that individuals who were higher in Neuroticism were more vigilant and engaged in more self-directed behaviours while participating in cognitive research [19]. Test anxiety, known to negatively impact performance on intelligence tests, is more common in high Neuroticism humans [4]. Despite showing signs of anxiety during testing, high Neuroticism chimpanzees did not perform more poorly than other chimpanzees. Having learned the importance of test taking over a lifetime [29], the test anxiety effect may reflect a tendency in humans to assign greater meaning to testing outcomes.

Openness was repeatedly associated with performance and participation. Most tellingly, chimpanzees high in Openness remained interested even when they were no longer rewarded, despite the fact that this took time away from opportunities to forage for free rewards. Openness was not associated with every measure of performance, however. Thus, while Openness partly overlaps with cognitive ability, Openness is also related to higher participation and curiosity about, and interest in, something intrinsic to the tasks themselves. These associations position chimpanzee Openness, like human intellect [2], close to a need for cognition.

Our findings are similar to what has been demonstrated in humans, particularly the connections between Conscientiousness and achievement [3], and Openness and need for cognition [9]. Nevertheless, these studies were conducted with only a single group of chimpanzees. Future studies should be conducted in different, large groups. Moreover, the evidence on the covariance of personality and performance has been disproportionately focused on chimpanzees. The attributes shared between human and chimpanzee intellect suggest that the roots of human achievement, intelligence and personality run far deeper than our own taxonomic family. To understand how far back these

commonalities stretch, we need to study personality in concert with engagement and performance in other intelligent species.

Ethics. Prior to conducting this work, D.M.A. obtained ethical approval from the University of Edinburgh Biological Services Ethical Review Committee (AWERB no: OS04-14) and the Budongo Trail Scientific Committee.

Data accessibility. The datasets supporting this article are available on the Dryad Digital Repository at http://dx.doi.org/10.5061/dryad.2v075 [30].

Authors' contributions. D.M.A. conceived of the study, participated in the design of the study, collected data and carried out the statistical analyses; E.K.W. and R.S. participated in the design of the study, collected data and provided materials; M.T. provided materials; A.W. conceived of the study, participated in the design of the study and provided materials. All authors helped draft the manuscript and gave final approval for publication.

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2.2 Multiple associations between personality, participation, and performance

In these studies, we found that high Conscientiousness chimpanzees were more likely to remain as participants in touchscreen testing experiments, more likely to attempt to interact with the touchscreen, and more precise in their touch responses. In study 1, high Conscientiousness individuals were faster and more accurate, but their accuracy was no better after controlling for experience. These associations with performance were also not found in study 2. These conditional associations between Conscientiousness and accuracy in these chimpanzees are similar to what we would expect to see among high Conscientiousness humans, as well: greater diligence, more self-control, and higher achievement which is not due to greater inherent intelligence.

Extraversion was also frequently associated with the variables in these tasks, though the associations between Extraversion and both performance and participation were not always consistent, or present where we would have expected to find them. High Extraversion chimpanzees were faster to respond, in all speed measures of both study 1 and study 2, which is consistent with the literature in humans (Chamorro-Premuzic & Furnham, 2006). Additionally, Extraversion was associated with higher accuracy in study 1 (when experience was controlled for), and also associated with spending more time in the research areas in study 3. However, Extraversion's relevance was not always apparent, as there was no association between Extraversion and accuracy in study 2, and it was the low Extraversion individuals who spent the most time interacting with the touchscreen in study 3.

Extraversion appears to be related to performance, particularly speed, but while it has been suggested that Extraversion is linked to motor mechanisms of the underlying biological substrate, insufficient evidence exists to support this claim, and this explanation should be viewed as a theory. Finally, why high Extraversion individuals were interested in some aspects of these tasks but not others is difficult to explain with these data.

The personality dimensions of Openness, Agreeableness, and Dominance were also implicated. Openness was repeatedly associated with interest and performance when the tasks gave rewards, though not in every model. In study 1, Openness was associated with higher participation and faster response times, but not accuracy. In study 2, Openness was associated with accuracy and greater engagement, but not response time. Moreover, high Openness was associated with unrewarded interest in the touchscreen apparatus, though only as measured through time spent at the screen.

Low Agreeableness individuals had faster response times in study 2, but otherwise the dimensions was not associated with performance. High Agreeableness individuals were less likely to drop out in study 1, and more likely to make individual approaches to the screen in study 3, despite the frequent presence of other chimpanzees in the research pods during this part of the study. Dominance was implicated in a few analyses: higher Dominance individuals participated more in study 1 and showed slower response times in study 2, but no interpretable pattern emerged. Similarly, Neuroticism was only associated with reduced engagement in study 1 and faster response times in study 2. Ultimately, there were not enough

significant results to interpret the role that either Dominance or Neuroticism might have played.

Comparing this study to other work in the literature, our results compare favourably to what others have found. High Openness primates appear to be more interested in novel objects (Massen et al., 2013), problem solving (Hopper et al., 2013), learning (Morton, Lee, & Buchanan-Smith, 2013), and now a variety of touchscreen tasks. Openness could be seen as strongly related to a need for cognition, and both have been related to general intelligence in humans (Von Stumm, Hell, & Chamorro-Premuzic, 2011), but Openness itself should not be viewed as a proxy for general intelligence.

Conscientiousness (or persistence (Massen et al., 2013) or attentiveness (Morton, Lee, & Buchanan-Smith, 2013)), has not been clearly linked to better performance in other studies and species. The strength of our study's longitudinal approach is most easily visible in this light. On the other hand, Hopper et al. (2013) found more consistent, strong associations between problem solving success and a chimpanzee personality domain not identified in this study: Methodical. From the name, the reader would be inclined to associate Methodical with Conscientiousness. But, this dimension was composed of two items, 'methodical' and 'self-caring', and it was not certain that the dimension was distinct enough to extract as a separate factor (Freeman et al., 2013). In both name and constituent items, methodical has similarities with Conscientiousness, and considering our results, the most parsimonious explanation is that Methodical taps into many of the same psychological substrates as Conscientiousness.

As indicated, many of our remaining results are difficult to interpret, and we hesitate to make unjustifiable extrapolations. Our results concerning Extraversion may be the most tempting to over interpret. It may be that high Extraversion individuals were biased by the social-spatial environment of the research areas to participate more during certain phases. A reviewer of this paper suggested we discuss the social environment surrounding the experiments. As described in the final revision of the paper, there was no manipulation of the environment, and due to the nature of the enclosure, individuals were always tested as part of a group. So while many chimpanzees moved in and out of the research areas during testing, and sometimes these areas were full of chimpanzees, there were only a few instances when more than one participant tried to interact with the touchscreen at a time. Manipulation of social circumstances are a heavily researched area of study in chimpanzee cognition, and it is likely that situational social factors do interact with personality. Unfortunately, grappling with this question in the context of this study would require high-resolution location data along with social network data, which we did not have access to.

However, we wish to emphasize that even in large humans sample and meta-analyses, studies of covariation between intelligence, personality, and achievement are not always consistent (Chamorro-Premuzic & Furnham, 2014). Our results are broadly in agreement with the human literature and the existing literature on nonhuman primates. However, our sample sizes were small compared to what one might see in the human literature, and while repeated observations leant additional power to the study, it is likely that we did not have the power to detect smaller effects.

An additional issue with this study and others is the use of overly specific and/or under validated tasks. As mentioned, Morton, Lee, and Buchanan-Smith (2013) used tasks which relied on associative learning, a specific, simple capability. On the other hand, Hopper et al. (2013) and Massen et al. (2013) used "puzzle boxes" that assessed chimpanzees' problem solving abilities. These tasks require intelligence to solve, but it is not clear whether these tap into general intelligence or specific domains, and if they do tap into specific domains, which ones.

Overall, this study is not an exception. While validity was improved by testing a variety of relations in study 1, the precise breadth of intelligence tested during this study remains an open question, unknowable from these data alone. In study 2, our task initially relied on associative learning, and though plans had been drawn up to extend the paradigm, the participants did not show sufficient proficiency to progress to a non-associative version of the task. All these tasks are testing intelligence, but there were not designed to test any specific domain, for example, numerical competence. A superior battery would be one which was designed to test all the known domains of primate intelligence. One of the most widely used instruments, the Primate Cognition Test Battery (Herrmann et al., 2007) is a strong model, but does fall short if one wants to study learning over time. Quick and reliable assessment is very important, but our study demonstrates that significant individual differences in performance and motivation over time exist in chimpanzees, and these differences should not be neglected.

3 Rhesus macaque personality and performance on a serial cognitive touchscreen task

3.1 Extending the framework

This chapter presents work which complements our work in chapter 2; the background and motivations for the two chapters were very similar. However, the experiment under study in this chapter benefits from much greater control. The laboratory setting of this work allowed us to fix several degrees of freedom that are not frequently under experimenter control, at least not at the same time.

All animals in this study were highly trained, beyond the point where we would see any noticeable improvement in performance over the course of the study. The macaques were thus experts with the particular task, the Simultaneous Chaining (SimChain) paradigm (Terrace, 2005) and would display peak performance by the end of each experimental session. Expert participants are used in human perceptual research (Tanaka & Curran, 2001) and some animal cognition work (Matsuzawa, Tomonaga, & Tanaka, 2006), but infrequently found in animal personality research because of difficulties with sample size and power. To the best of our knowledge, no study of animal personality and cognition has worked with expert participants.

Confounding social circumstances were eliminated as possible influences on these individuals. While the macaques lived in a social colony setting, the macaques were isolated from one another while in the operant testing chambers. No external

stimuli could influence their performance. Sex was also ruled out as a confound because the sample was entirely male.

A key difference between this study and others (notably, the others in this manuscript), is that the animals under study were rhesus macaques. The rhesus macaque diverged from the common ancestor of chimpanzees and humans around 25 million years ago (Gibbs et al., 2007). Macaques are some of the most common research subjects found in biomedical labs because they are seen as useful surrogates for humans in neuroscience, epidemiology, drug development, and other fields of research. Consequently, macaques have also been studied in hundreds if not thousands of animal behavior and animal cognition projects, and their cognitive abilities are well-known.

Similarly, macaque personality has been repeatedly described throughout the development of the animal personality literature (Capitanio, 1999; Chamove et al., 1972; Figueredo, Cox, & Rhine, 1995; Stevenson-Hinde & Zunz, 1978), although arguably the most complete, and certainly the most relevant to this study, structure of rhesus macaque personality posits six dimensions: Confidence, Openness, Dominance, Friendliness, Activity, and Anxiety (Weiss, Adams, Widdig, et al., 2011).

Having described the advantages of this sample, we had two major goals in this study. First, we wished to further extend the work on cognition and personality to macaques. Unsurprisingly, covariation in rhesus macaque cognition and personality is not entirely unstudied (Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980), but the

present study benefits from our use of comprehensive scores derived from the HPQ and the SimChain task, which is difficult by animal cognition standards.

Second, we wished to use the granularity of our data and existing, validated models of learning (Jensen, Altschul, Danly, & Terrace, 2013; Thurstone, 1918) to test for specific differences in performance, and determine if these differences were associated with personality. Thus, nine macaques were rated for personality, and using modelling techniques which could assess both rate of learning and plateau accuracy, we related these personality dimensions to individual differences in performance on a 4-item SimChain task.

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Serial Cognition and Personality in Macaques

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Abstract - We examined the associations between serial cognition and personality in rhesus macaques (*Macaca mulatta*). Nine macaques were tested on a simultaneous chaining task to assess their cognitive abilities. They were also rated for personality traits and scored according to a previously extracted six component structure derived from free-ranging rhesus macaques. Friendliness and Openness were positively associated with good performance on three measures of accuracy on the serial learning task: Progress, Error, and Rewarded (i.e., correctly completed) Trials. Faster Reaction Times were associated with lower Friendliness and higher Confidence, as well as higher Openness when only correct responses were analyzed. We also used regularized exploratory factor analysis to extract two, three, four, five, and six factor structures, and found consistent associations between accuracy and single factors within each of these structures. Prior results on intelligence in other nonhuman primate species have focused on basic intelligence tests; this study demonstrates that more complex, abstract cognitive tasks can be used to assess intelligence and personality in nonhuman primates.

Keywords - Primates, Rhesus macaques, Personality, Individual differences, Serial cognition, Comparative cognition

The study of individual psychological differences in animals originated with Pavlov, who classified personality as learning characteristics among his dogs (Pavlov, 1908/1941). In primates, Yerkes (1939), Crawford (1938), and Hebb (1946) all worked with the same group of chimpanzees, and all three found evidence for personality, from both observer ratings and behavioral codings. Early researchers did not restrict their studies to captive animals; free-ranging Japanese macaques (Itani, 1957) and chimpanzees (Goodall, 1990) were also described as having distinct personalities.

Personality describes individual differences in behavior that are stable over time and across different contexts (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Individual differences in cognitive abilities differ in that they rely on quantifying performance (Griffin, Guillette, & Healy, 2015), e.g., percentage correct out of a set number of trials, or average reaction time. Serial cognition is one faculty that has been studied as a means of understanding how animals learn and manipulate complex information (D'Amato & Colombo, 1990). However, few studies of serial cognition, as well as animal cognition more broadly (Griffin et al., 2015), have addressed where individual differences in performance come from, as the focus has typically been on the abilities of the species and not those of individuals (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Terrace, 1993). The exceptions include Vonk and Povinelli (2011), who found that different chimpanzees excelled in social and physical tasks, except for one individual who performed well at both, and Herrmann, Hernández-Lloreda, Call, Hare, and

Tomasello (2010), who reanalyzed their earlier data to assess individual differences with factor analytic techniques. The majority of these studies have focused on a single species: the common chimpanzee.

The study of animal personality, on the other hand, has flourished in the last two decades. One way in which species personalities can be described is by quantifying traits along a small number of dimensions. In humans this gave rise to the "Big Five" or "Five-Factor Model," which incorporates dimensions usually named Neuroticism, Extraversion, Openness to experience, Agreeableness, and Conscientiousness (McCrae & John, 1992). Chimpanzees, which share a recent common ancestor with humans, possess six dimensions, five resembling the human personality dimensions, plus the dimension Dominance (King & Figueredo, 1997). On the other hand, rhesus macaques, representatives of an older ancestor, also have six personality dimensions, that differ some from the chimpanzee and human dimensions: Anxiety, Activity, Openness, Friendliness, Confidence, and Dominance (Weiss, Adams, Widdig, & Gerald, 2011).

Within-species personality variation may drive the variability within cognitive capacities. Female rhesus macaques with a tendency towards exploratory behaviors acquired operant responses 50% more often than less adventurous subjects (Coleman, Tully, & McMillan, 2005); exploratory behaviors in mice covaried with learning differences (Matzel et al., 2003), and chickadees that were slow to explore were more accurate during testing, but did not learn the experimental task more quickly than other chickadees (Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015). The common attribute of these studies – 'exploration' – calls to mind two human personality dimensions: Extraversion and Openness. However, most research has associated animal personality with behavior (e.g., Capitanio, 1999; Konečná et al., 2008; Pederson, King, & Landau, 2005), rather than cognitive ability. Moreover, prior research has been largely observational (Konečná et al., 2008; Pederson et al., 2005), not experimental. Meanwhile, complex, repeatable tasks have been realized in captive environments thanks to modern computing power and equipment (Fagot, Gullstrand, Kemp, Defilles, & Mekaouche, 2014). These tasks provide rich data that permit stronger inference about cognitive function than earlier operant techniques.

Recent studies have begun bridging the gaps between cognitive and personality psychology (Herrelko, Vick, & Buchanan-Smith, 2012; Morton, Lee, & Buchanan-Smith, 2013) with factor analytic approaches common to personality and intelligence research (Herrmann et al., 2010; Hopkins, Russell, & Schaeffer, 2014). Intelligence is a general cognitive ability that underlies individual differences in performance on mental tests, such as Raven's Standard Progressive Matrices and the National Adult Reading Test (Deary, 2001). This general factor of intelligence or '*g*' factor is widely used in individual differences research, and moderately sized relationships have been found between measures of *g* and the Five-Factor Model in humans (Austin, Deary, & Gibson, 1997). In particular, high Openness to experience has been repeatedly linked to high *g* factor scores (DeYoung, 2014).

The majority of studies on general primate intelligence have been meta-analyses (Deaner, Van Schaik, & Johnson, 2006; Reader, Hager, & Laland, 2011; Schmitt, Pankau, & Fischer, 2012) that identify intelligence differences between species. Herrmann et al. (2010) compared chimpanzees with human children; principal components analyses indicated that a 'Spatial' and a 'Physical-Social' factor best explained the structure of differences in chimpanzee performance. Subsequently, Hopkins et al. (2014) used the Primate Cognition Test Battery (Herrmann et al., 2010) modeled performance on the task as arising from a single *g* factor, with four constructs beneath. The chimpanzee *g* factor was heritable (Hopkins et al., 2014), as has been shown in humans (Davies et al., 2011; Deary, Spinath, & Bates, 2006).

Serial cognition has been studied in many species with many paradigms; varying demonstrations of proficiency have been displayed across studies (McGonigle & Chalmers, 2006). The Simultaneous Chaining (SimChain) paradigm is one of the most difficult tests of serial cognition: the commonly used serial cognition paradigm, Transitive Inference (TI), only requires binary responses, whereas SimChain requires multiple successive, correct responses for an animal to be rewarded. Monkeys' behavior in completing SimChain trials is known for defying traditional chaining theory (Ebbinghaus, 1913/2014). Instead of learning associations between successive items, monkeys learn the ordinal positions of individual items, encoding them in a spatial representation (Chen, Swartz, & Terrace, 1997).

Serial intelligence is a broadly applied, flexible ability: despite their differences in difficulty, the SimChain and TI paradigms share a common mental representation (Jensen, Altschul, Danly, & Terrace, 2013). Transitive reasoning is in turn linked to symbolic manipulation (D'Amato & Colombo, 1990), social dominance and navigation in primate hierarchies (Paxton et al., 2010), and language (Jensen et al., 2013). These links make SimChain a strong candidate for testing general cognitive ability in animals.

While the evolution of serial cognition is well documented (McGonigle & Chalmers, 2006), why individual personalities have been selected for remains an open question (Bouchard & Loehlin, 2001). Moreover, the evolutionary genetics underlying individual differences in intelligence and personality need not be very similar. If the contributions of gene and environment differ between personality and intelligence (Penke, Denissen, & Miller, 2007), then how should we expect animals' personalities to vary with cognitive abilities? In nine rhesus macaques, we collected cognitive and personality data, and in a series of exploratory analyses we examined connections between personality and serial cognition, with the expectation that Openness, and possibly other macaque personality dimensions, would be associated with performance on the SimChain task.

Method

Subjects

Nine male captive-born rhesus macaques, aged 12 to 16 years, and housed at the New York State Psychiatric Institute, performed a SimChain task and were evaluated for personality. The colony was maintained in accordance with guidelines issued by the National Institutes of Health and the Institutional Animal Care and Use Committees at the New York State Psychiatric Institute and Columbia University. Macaques were individually housed in adjoining cages at the time of the study, but had been pair housed previously. Macaques were given water ad libitum, and fed commercial primate biscuits and varied fresh fruits and vegetables daily, in addition to any pellets they received as rewards in experimental tasks.

Apparatus

The apparatus was identical to that used in prior studies (Jensen et al., 2013). Testing took place in chambers housed in sound-attenuated booths. Chambers were equipped with speakers, and a pellet dispenser (Med Associates; pellets by BioServ, 190 mg). A computer with a touch-sensitive monitor presented stimuli and detected responses.

Procedure

The SimChain paradigm presents an ordered list as a simultaneously displayed set of images on a touchscreen monitor. A trial is completed by selecting each stimulus in the correct order (see Figure 1; Terrace, 1993). In this experiment, subjects had to learn a novel four-item list composed of arbitrary color images, each day. Subjects were given 40 trials to learn each list, which could only be accomplished through trial and error. On successful trials, subjects were rewarded with a banana pellet. On unsuccessful trials they received a 4 s timeout. We gathered 20 days of data, that is, 20 sessions of 40 trials each.

Because subjects had been extensively trained on SimChain tasks, no task learning effects were expected to confound results. Subjects could be expected to display their asymptotic level of performance.

Personality Ratings

Subjects were independently rated by 10 animal care volunteers using the Hominoid Personality Questionnaire (Weiss et al., 2009). The questionnaire consisted of 54 adjectives followed by 1 to 3 sentences defining adjectives in terms of everyday nonhuman primate behaviors. Items were rated on a 7-point scale. Raters were familiar with subjects prior to evaluating them, but unaware of the details of

individual subjects' performance. Raters had between 6 months and 3 years of experience with the animals; each rater typically spent several hours, one day a week, looking after the animals within the colony setting.

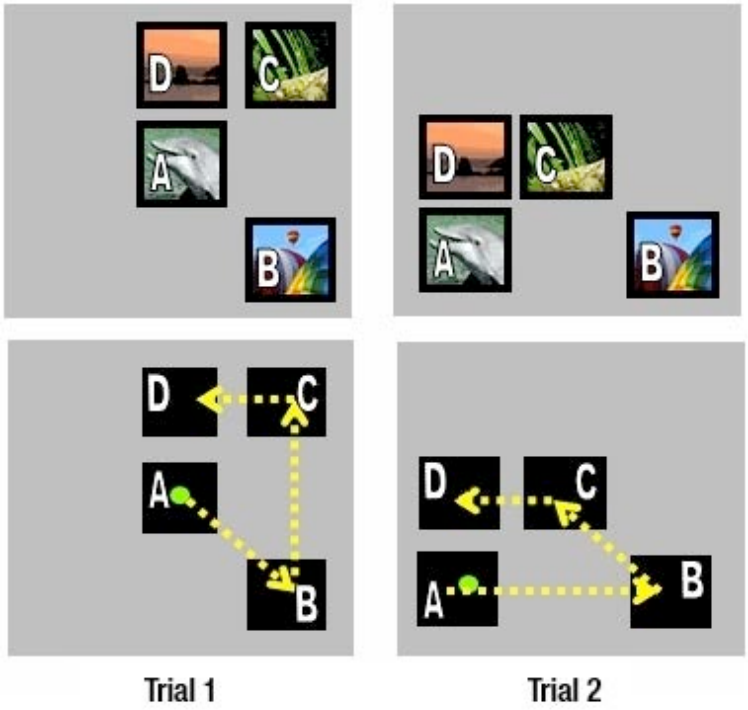

Figure 1. The Simultaneous Chaining paradigm. The task was to touch the items in the prescribed order, regardless of their positions on the screen. An example of a 4-item list is shown in two different, random arrangements, as might appear during any trial in a session. The top row shows the arrangement of ordered pictures, and the bottom row indicates the correct path of selection.

Analysis

The R programming language (version 3.2.1; R Core Team, 2015) was used for all correlation and regression analyses, using the 'psych' (Revelle, 2015), 'nlme' (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team (2015), 'lme4' (Bates, Maechler, Bolker, & Walker, 2015), and 'car' (Fox & Weisberg, 2011) packages. Regularized exploratory factor analyses (Jung & Lee, 2011) were carried out in MATLAB 2014a, using custom code by Sunho Jung.

Results

Interrater Reliability

Interrater reliabilities of personality items were calculated from all animals and all raters using intraclass correlations (Shrout & Fleiss, 1979) *ICC*(3, 1) and *ICC*(3, *k*). The items 'cautious,' 'defiant,' 'independent,' and 'stingy/greedy' had *ICC*s less than zero and were removed from further analysis. The items 'autistic' and 'unperceptive' were omitted because both were removed from an earlier study for being unreliable and thus not included in the definitions of the components (Weiss et al., 2011). The remaining items' *ICC*s ranged from 0.009 to 0.290 for *ICC*(3, 1), and 0.079 to 0.801 for *ICC*(3, *k*).

Personality and Performance

Average questionnaire ratings were used to compute domain scores from the unit-weighted matrix based on previously derived component loadings (Weiss et al., 2011; Table 1). Performance was measured using three measures of trial-by-trial accuracy. *Rewarded trials* reflect the binary successes and failures across each subject's trial-by-trial performances: to be rewarded, a subject must complete a full SimChain trial without error. *Progress* quantifies how far into the list the subject made it on any given trial, before either making an error or completing the trial. *Error* is defined as the amount of deviation, from the next correct response, in a subject's terminal choice. Error can be either positive or negative: If the subject makes forwards error, jumping ahead in the chain, the Error is positive. If the subject makes a backwards Error, it is negative. If the subject presses each item in the correct order and completes a trial successfully, the Error is 0. Error and Progress for each of the nine monkeys is shown in Figures 2 and 3, respectively.

Reaction time (RT) is the natural logarithm of the interval between the onset of the visual stimuli and the first response. SimChain completion utilizes a series of planned responses (Scarf, Danly, Morgan, Colombo, & Terrace, 2011), but apart from the pause before the initial response, wherein the chain planning pauses occur depends on the individual animal. We analyzed the first response RT for only correct responses, as well as the RT for all first responses, to search for speed-accuracy trade-offs (Prinzmetal, McCool, & Park, 2005).

Correlations between personality and performance (averaged across trials and sessions) are shown in Table 1. Friendliness was significantly positively correlated with Rewarded trials and Progress; negatively correlated with Error. Openness was significantly correlated with Progress and Error, in the same directions as with Friendliness. No significant correlations were found between personality domains and either RT measure.

Table 1

Correlations among Personality and Averaged Performance Variable

	Anx	Act	Frd	Dom	Opn	Con	Rwd	Err	Prg	RT
Act	0.57									
Frd	-0.12	0.49								
Dom	0.70	0.85	0.08							
Opn	0.79	0.63	0.33	0.50						
Con	-0.53	0.31	0.57	0.15	0.26					
Rwd	0.21	0.55	0.71	0.26	0.65	0.38				
Err	-0.25	0.53	-0.70	-0.28	-0.67	-0.34	-0.99			
Prg	0.24	0.56	0.73	0.27	0.67	0.35	1.00	-0.99		
RT	0.07	0.24	0.28	0.14	-0.07	-0.09	-0.09	0.03	0.05	
RT1	-0.12	0.19	0.17	0.09	-0.25	0.08	-0.07	0.02	0.03	0.91

Note. Correlations of $| r | > 0.66$ are significant at the $\alpha = 0.05$ level. Anx = Anxiety, Act = Activity, Frd = Friendliness, Dom = Dominance, Opn = Openness, Con = Confidence, Rwd = Rewarded trials, Err = Error, Prg = Progress, RT = all reaction times, RT1 = reaction times on trials which were correctly completed.

Regression Analyses

Simple correlations between averages fail to capture the nuance in individuals' performance. For example, both Error (Figure 2) and Progress (Figure 3) demonstrate learning curves and asymptotic plateaus in performance, which differ between animals. To explore personality's relationship with

performance in more detail, we modeled each performance metric including personality predictors based on the strength of associations seen in the correlation matrix.

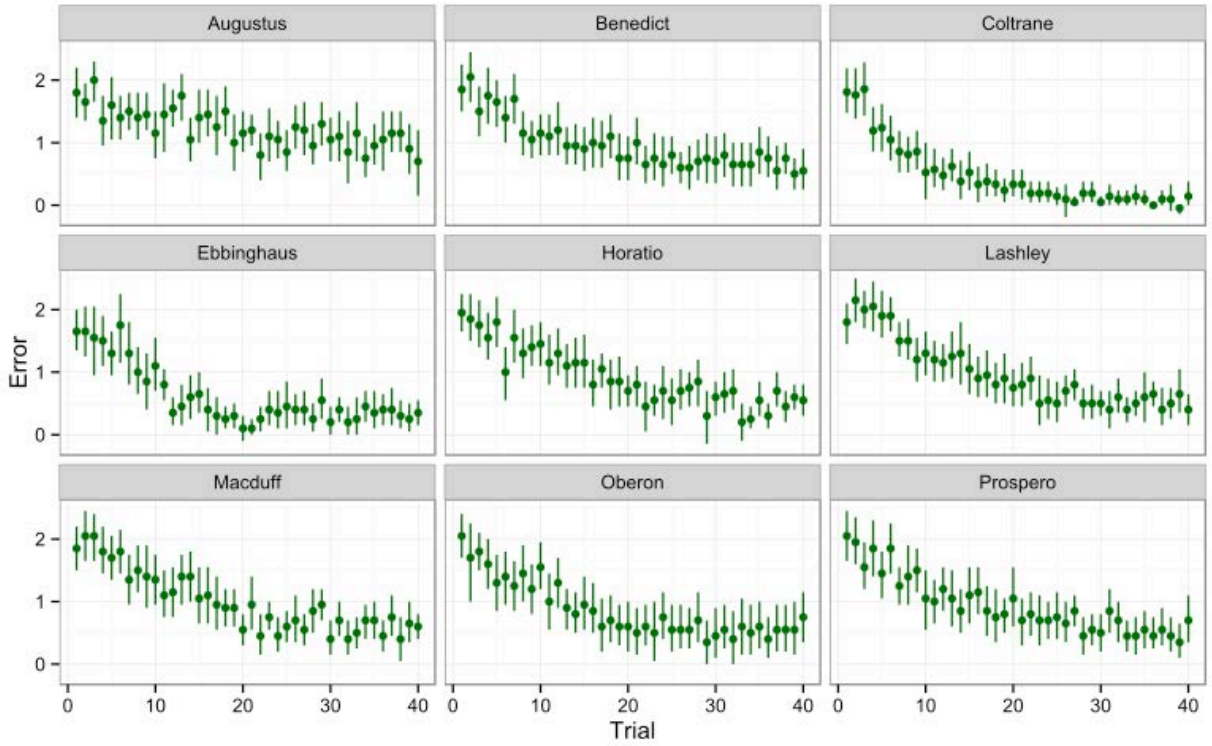

Figure 2. Average Error data from 20 sessions of 40 trial SimChain, from 9 monkeys. Bars indicate standard errors.

Error

If one wishes to model Error with linear regression, the Error data must first be transformed, because they are non-linear (Figure 2). This poses a challenge because Error can be both positive and negative, thus log-transformation is not appropriate. Fortunately, Yeo-Johnson transformation, which was designed for and tested on cases such as ours, handles negative values (Yeo & Johnson, 2000). We constructed a series of linear mixed models, using a forward selection approach, starting with a null model which included a trial number variable and intercept. Results of our model selection are shown in Table 2.

Log-likelihood indicated that model 7 was the best fit to the data, while the small-sample corrected Akaike Information Criterion (AICc) indicated that model 6 was the best fit. The Bayesian Information Criterion (BIC) indicated that the null model was the best fit, which was a consistent prediction across all our models. The BIC is more strongly biased towards models with fewer degrees of freedom, for as the sample size increases, the probability that BIC selects the correct model approaches 1 (Vrieze, 2012). For smaller sample sizes, BIC necessarily performs less well on average, so while we continued to calculate it for all models for diagnostic purposes, we did not factor it into our selection procedures.

The details of models 6 and 7 are shown in Table 3. Both models consistently show that higher Openness was significantly associated with a smaller starting error, itself an indicator of better performance. The interaction between Friendliness and Trial was also significant in both models, similarly suggesting that Friendliness was associated with smaller error as sessions progressed. Outside of the interaction, Friendliness was not a significant predictor, though it did appear to marginally improve

the fit of the model. The effect size of the Openness coefficient was also larger than either Friendliness coefficient.

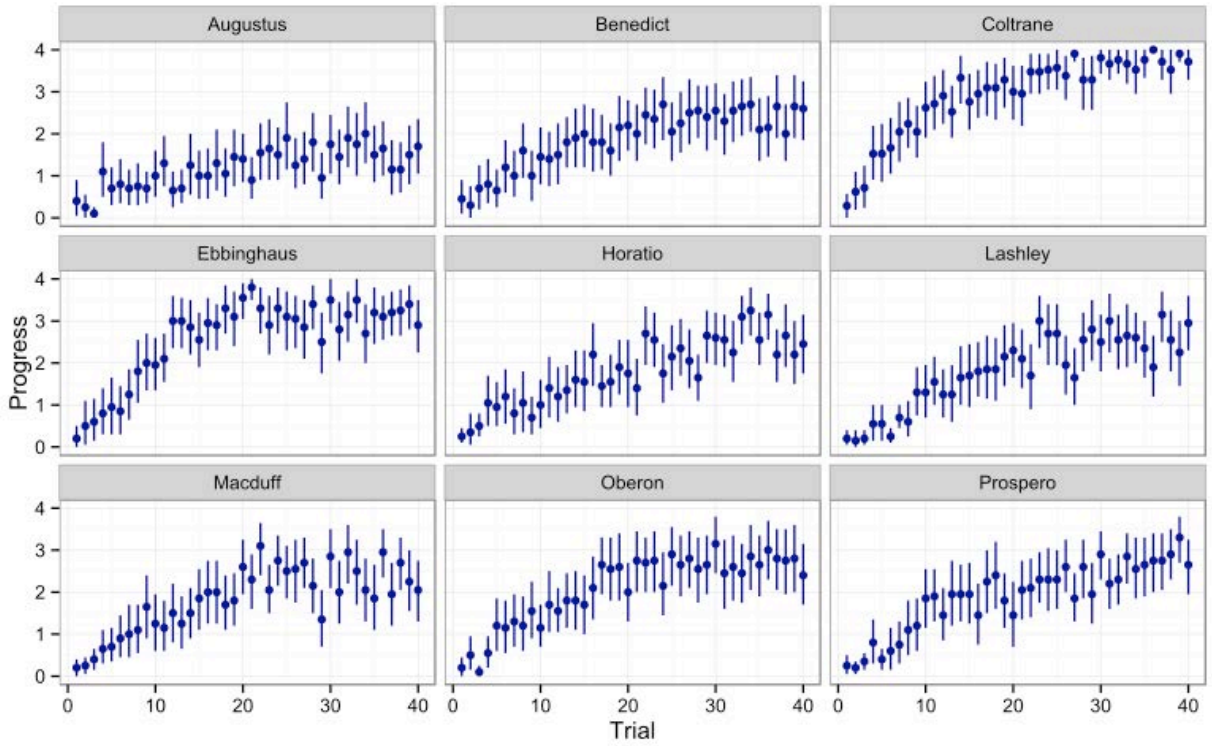

Figure 3. Average Progress data from 20 sessions of 40 trial SimChain, in 9 monkeys. Bars indicate standard errors.

Table 2

Model Selection Results for Regressions Predicting Transformed Error Variable

Model Number	Variables	df	AICc	BIC	LogLik	ΔLogLik	RM
0	(Trial, Incercept)	9	18117.0	**18179.0**	-9049.5		
1	Frd	10	18117.0	18185.8	-9048.5	1.0	0
2	Opn	10	18115.1	18183.9	-9047.5	1.0	1
3	Frd * Trial	10	18112.5	18181.4	-9046.2	1.3	2
4	Opn * Trial	10	18117.9	18186.7	-9048.9	-2.7	3
5	Frd * Trial, Frd	11	18113.5	18189.2	-9045.7	0.5	3
6	Frd * Trial, Opn	11	**18110.1**	18185.8	-9044.0	1.7	5
7	Frd * Trial, Opn, Frd	12	18111.8	18194.4	-9043.9	**0.1**	6

Note. Bolding indicates the best model, according to the procedure. df = degrees of freedom, AICc = Akaike Information Criterion corrected for small samples, BIC = Bayesian Information Criterion, LogLik = Log-likelihood, ΔLogLik = difference in log-likelihood between current model and last best fitting model, RM = the reference model for the ΔLogLik comparison.

Table 3

Details of Linear Regression Models of Interest, Predicting Error from Personality

	Model 6			Model 7		
Predictor	*b*	*95% CI*	χ^2	*b*	*95% CI*	χ^2
(Intercept)	3.01	[1.72, 4.30]		3.24	[1.72, 4.75]	
Trial	0.02	[-0.01, 0.05]	556.80 ****	0.01	[-0.02, 0.05]	600.00 ****
Opn	-0.42	[-0.76, -0.08]	5.71 *	-0.39	[-0.74, -0.03]	4.59 *
Frd				-0.09	[-0.39, 0.23]	3.34
Frd * Trial	-0.01	[-0.02, -0.00]	10.80 ****	-0.01	[-0.02, -0.00]	7.72 **

Note. *p*-values are from Wald's χ^2 tests. CI = confidence interval, Opn = Openness, Frd = Friendliness.
*$p < 0.05$. **$p < 0.01$. ****$p < 0.001$.

Progress

Progress displays a similar curve as Error (*cf.* Figures 2 and 3), but unlike Error, it does not take negative values. However, Progress on the SimChain task can be modeled using Thurstone's learning curve (Jensen et al., 2013), so rather than linearize the Progress data, we modeled Progress with a non-linear logistic regression. A simple logistic growth curve has three parameters, and is defined:

$$f(x) = \frac{L}{1 + e^{-k(x-x_0)}} \qquad [1]$$

where L is the maximum value or asymptote of the curve, k is the steepness of the curve, and x_0 is the x-value midpoint of the curve, also known as a scaling parameter.

We used a forward selection approach to model building, jointly inputting personality dimensions as predictors of two logistic parameters: asymptote – L, and steepness – k (Table 4). The model including Friendliness alone was the best fit, but only in the most marginal sense, as the AICc and log-likelihood values were extremely close to those generated by model 2, wherein Openness was the lone personality predictor. Fit became considerably worse when both Friendliness and Openness were included, but we still wished to examine if and how their contribution to the model might change in each other's presence.

All three non-null models are described in Table 5. Friendliness was positively and significantly associated with the asymptotic level of performance; Openness negatively and significantly associated with the steepness coefficient. Due to software limitations, steepness needed to be modeled as 1 / k, thus higher Openness was associated with a steeper, and faster, rate of learning.

Rewarded Trials

Monkeys were reinforced with food only after correctly completing a full SimChain. To model personality's impact on this binary variable, we fitted a generalized linear mixed model, with a binomial logistic link function. Model building was again carried out with a forward selection procedure, and because of the simplicity in adding individual predictors, we chose to input a broader choice of personality predictors (Table 6).

Models 5 and 7 appeared to be the best fit, according to AICc and log-likelihood, respectively. Comparing those two models (Table 7) revealed that when only Friendliness and Openness were included, both were positively associated with subjects' rate of reward. However, when all personality

predictors were included, only Confidence showed a significant (and positive) relationship with rate of reward.

Table 4

Model Selection Results for Regressions Predicting Progress Variable

Model Number	Variables	df	AICc	BIC	LogLik	ΔLogLik	RM
0	(Intercepts only)	10	26224.8	**26293.7**	-13102.4		
1	Frd	12	**26222.6**	26305.2	-13099.3	**3.1**	0
2	Opn	12	26222.8	26305.4	-13099.4	-0.1	1
3	Frd, Opn	14	26237.6	26333.9	-13104.8	-5.5	1

Note. Bolding indicates the best model, according to the procedure. See Table 2 for explanation of abbreviations.

Table 5

Details of Non-Linear Regression Models of Interest, Predicting Progress

	Model 1			Model 2			Model 3		
Predictor	*b*	*95% CI*	*t*	*b*	*95% CI*	*t*	*b*	*95% CI*	*t*
Asymptote									
(Intercept)	-0.30	[-2.27, 1.66]	-0.30	2.34	[-0.21, 4.88]	1.80	-5.70	[-8.99, -2.35]	-3.35 ****
Friendliness	0.74	[0.25, 1.23]	2.98 ***				1.16	[0.50, 1.82]	3.45 ****
Openness				0.08	[-0.58, 0.75]	0.24	0.98	[0.16, 1.79]	2.35 *
Steepness									
(Intercept)	-1.47	[-9.71, 6.76]	-0.35	18.20	[11.50, 24.8]	5.34 ****	14.50	[3.42, 25.5]	2.57 *
Friendliness	1.72	[-0.31, 3.75]	1.66				1.00	[-0.92, 2.92]	1.02
Openness				-3.41	[-5.08, -1.73]	-3.99 ****	-3.53	[-5.29, -1.77]	-3.93 ****
Midpoint	9.68	[8.66, 10.7]	18.60 ****	9.63	[8.54, 10.7]	17.30 ****	8.80	[8.27, 9.33]	32.60 ****

Note. p-values are from Welch's *t* tests.
*$p < 0.05$. **$p < 0.01$. ***$p < 0.005$. ****$p < 0.001$.

Table 6

Model Selection Results for Regressions Predicting Rewarded Trials

Model Number	Variables	df	AICc	BIC	LogLik	ΔLogLik	RM
0	(Trial, Intercept)	4	7462.1	**7489.6**	-3727.0		
1	Opn	5	7458.7	7493.1	-3724.3	2.7	0
2	Frd	5	7456.7	7491.2	-3723.4	0.9	1
3	Con	5	7462.6	7491.1	-3726.3	-2.9	2
4	Act	5	7460.1	7494.6	-3725.1	-1.7	2
5	Frd, Opn	6	**7453.2**	7494.5	-3720.6	2.8	2
6	Frd, Opn, Act	7	7455.2	7503.4	-3720.6	0.0	5
7	Frd, Opn, Act, Con, Dom, Anx	10	7455.3	7524.1	-3717.6	**3.0**	5

Note. Bolding indicates the best model, according to the procedure. Con = Confidence, Act = Activity, Dom = Dominance, Anx = Anxiety. See Table 2 for explanation of all other abbreviations.

Table 7

Details of Binomial Regression Models of Interest, Predicting Rewarded Trials from Personality

	Model 5			Model 7		
Predictor	*b*	*95% CI*	*z*	*b*	*95% CI*	*z*
(Intercept)	-14.30	[-18.80, -9.86]		-22.80	[-30.50, -15.10]	
Trial	0.09	[0.08, 0.09]	30.70 ****	0.09	[0.08, 0.09]	30.70 ****
Anxiety				1.76	[-0.91, 4.43]	1.29
Activity				-0.20	[-2.00, 1.60]	-0.22
Confidence				2.45	[0.47, 4.44]	2.42 *
Dominance				-1.16	[-2.95, 0.63]	-1.28
Friendliness	1.52	[0.65, 2.39]	3.42 ****	0.39	[-0.89,1.68]	0.60
Openness	1.54	[0.45, 2.63]	2.76 **	1.97	[-0.03, 3.97]	1.93

*$p < 0.05$. **$p < 0.01$. ***$p < 0.005$. ****$p < 0.001$.

Reaction Time

We analyzed RT data with a series of linear mixed models. In light of the previous result and the generally weak correlations between personality and RT, we used a backward selection procedure, removing the lowest scored predictor from the previous model, for all models built on RT data. We first examined the fit of models predicting RT for all first responses (Table 8).

The log-likelihood indicated that model 1, featuring all personality predictors, was the best fit, but AICc suggested that removing Activity added a small improvement in fit. Comparing the two models' predictors directly (Table 9) yields consistent results. In model 2, removing Activity drastically increased the χ^2 scores of all predictors, but the two predictors which are significant in model 1, Confidence and Friendliness, were stronger than all other personality predictors in model 2. Confidence demonstrated a negative relationship, such that more confident monkeys tended to have lower, i.e., faster, reaction times. Friendliness had an opposite, positive relationship with reaction time; friendlier monkeys were slower to respond.

Table 8

Model Selection Results for Regressions Predicting Log Transformed RTs

Model Number	Parameters	df	AICc	BIC	LogLik	ΔLogLik	RM
0	(Trial, Intercept)	9	10689.3	**10751.2**	-5335.6		
1	All	15	10684.4	10787.6	-5327.1	**8.5**	0
2	Frd,Opn,Con,Anx,Dom	14	**10683.4**	10779.7	-5327.7	-0.6	1
3	Frd,Opn,Con,Dom	13	10684.3	10773.7	-5329.1	-2.0	1

Note. Bolding indicates the best model, according to the procedure. Con = Confidence, Act = Activity, Dom = Dominance, Anx = Anxiety. See Table 2 for explanation of all other abbreviations.

Only the correct first responses were separately analyzed, as well, for these two RT measures may tie into different processes (Prinzmetal et al., 2005). The models' log-likelihoods again suggested that model 1, containing all predictors, was the best fit (Table 10). On the other hand, model 3, containing

Friendliness, Openness, Confidence, and Dominance, was suggested to be the best fit by AICc. We directly compared these two models and the intermediate model (Table 11).

All three models indicated that Friendliness, Openness, and Confidence were significantly associated with RT on correct first responses. As in our models of all first responses, Friendliness was positively associated with RT, and Confidence negatively associated. Openness demonstrated a negative relationship with RT.

Table 9

Details of Linear Regression Models of Interest, Predicting RTs from Personality

	Model 1			Model 2		
Predictor	*b*	*95% CI*	χ^2	*b*	*95% CI*	χ^2
(Intercept)	3.85	[2.43, 5.27]		3.86	[2.34, 5.31]	
Trial	-0.011	[-0.013, -0.009]	51.50 ***	-0.011	[-0.013, -0.009]	57.90 ***
Anxiety	-0.60	[-1.08, -0.11]	1.32	-0.58	[-1.08, -0.09]	5.33 *
Activity	0.17	[-0.15, 0.49]	0.25			
Confidence	-0.91	[-1.28, -0.55]	5.71 *	-0.91	[-1.29, -0.54]	23.10 ***
Dominance	0.43	[0.11, 0.75]	1.66	0.52	[0.25, 0.79]	14.90 ***
Friendliness	0.56	[0.33, 0.79]	5.66 *	0.65	[0.46, 0.84]	44.50 ***
Openness	-0.43	[-0.79, -0.07]	1.45	-0.44	[-0.79, -0.09]	5.95 *

Note. *p*-values are from Wald's χ^2 tests.
*$p < 0.05$. ***$p < 0.001$.

Table 10

Model Selection Results for Regressions Predicting Log Transformed Rts on Only Correct Trials

Model Number	Parameters	df	AICc	BIC	LogLik	ΔLogLik	RM
0	(Trial, Intercept)	9	6217.3	6276.2	-3099.6		
1	All	15	6212.2	6310.3	-3091.0	8.6	0
2	Frd,Opn,Con,Anx,Dom	14	6210.6	6302.2	-3091.3	-0.3	1
3	Frd,Opn,Con,Dom	13	6209.2	6294.3	-3091.6	-0.6	1
4	Frd,Opn,Con	12	6214.8	6293.3	-3095.4	-4.4	1

Note. Bolding indicates the best model, according to the procedure. Con = Confidence, Act = Activity, Dom = Dominance, Anx = Anxiety. See Table 2 for explanation of all other abbreviations.

Sensitivity Analysis

To determine if our findings were unique to a six component structure, we extracted our own structures. Because we had only 9 subjects, four methods commonly used to choose how many factors to extract did not yield consistent results. Ruscio and Roche's comparison data, Horn's parallel analysis, Velicer's MAP criterion, and the acceleration factor, as well as two prior studies (Capitanio, 1999; Weiss et al., 2011), suggested anywhere from two to six factors.

Table 11

Details of Linear Regression Models of Interest, Predicting RTs on Correct Trials

	Model 1			Model 2			Model 3		
Predictor	*b*	*95% CI*	χ^2	*b*	*95% CI*	χ^2	*b*	*95% CI*	χ^2
(Intercept)	4.03	[2.24, 5.825]		4.03	[2.17, 5.89]		3.43	[2.33, 4.53]	
Trial	-0.009	[-0.011, -0.007]	39.60 ***	-0.009	[-0.013, -0.005]	38.90 ***	-0.009	[-0.013, -0.005]	37.60 ***
Anxiety	-0.30	[-0.92, 0.32]	0.91	-0.30	[-0.93, 0.34]	0.85			
Activity	0.15	[-0.264, 0.56]	0.49						
Confidence	-0.82	[-1.28, -0.35]	12.00 ***	-0.82	[-1.30, -0.34]	11.30 ***	-0.64	[-0.88, -0.40]	27.50 ***
Dominance	0.29	[-0.12, 0.70]	1.94	0.37	[0.03, 0.71]	4.44 *	0.22	[0.08, 0.35]	10.30 **
Friendliness	0.68	[0.39, 0.97]	20.80 ***	0.75	[0.50, 0.10]	34.90 ***	0.76	[0.49, 1.02]	32.00 ***
Openness	-0.85	[-1.30, -0.40]	13.80 ***	-0.84	[-1.29, -0.39]	13.50 ***	-1.03	[-1.36, -0.70]	37.10 ***

Note. *p*-values are from Wald's χ^2.
*$p < 0.05$. **$p < 0.005$. ***$p < 0.001$.

Since the interpretation of any single factor structure extracted from these data would be dubious, we used regularized exploratory factor analysis (Jung & Lee, 2011), a procedure developed for small samples, to separately extract 2, 3, 4, 5, and 6 factor structures. Salient loadings were defined as ≥ |0.6|, to minimize cross-loadings. Unit-weighted, varimax rotated matrices were compiled from the salient loadings for each solution. As in prior studies (e.g., Weiss et al., 2011), when more than one factor was salient for an item, the weight was assigned to the factor with the higher loading.

Within every solution, one factor correlated with subjects' averages of our accuracy measures. Which adjectives loaded onto these factors is shown in Table 12. The adjectives 'innovative' and 'inventive', which were each correlated with the averages of our performance measures (*r*s > |0.84|, *p*s < 0.05, after Holm-Bonferroni correction), were salient for all structures. 'Intelligent,' the third adjective to pass Holm-Bonferroni correction, was weighted on only three correlated factors. 'Curious' and 'decisive,' two adjectives correlated with Openness and Friendliness, pre-correction, were salient on three domains, as were 'individualistic,' 'independent,' and 'quitting,' items that were not part of Openness or Friendliness.

Across structures, performance metrics were compared to 20 factors. After Holm-Bonferroni correction, we found that correlations between the accuracy measures and the sixth factor of the six factor structure remained significant. Correlations also maintained significance with the second factor of the two factor structure. Significant correlations were not supported for Rewarded trials, Progress, or Error. These factors were composed largely of the same adjectives (Table 12), some of those explicitly noted in the preceding paragraph. Inclusion of adjectives like 'innovative,' 'inventive,' 'intelligent' and 'curious' represent behaviors associated with openness and intellect. 'Conventional' (negatively loaded), 'individualistic,' 'independent,' and 'decisive' emphasize assertiveness and individuality, monkeys that were extraordinary and whose personalities stood out to our raters. All-together, the traits associated with serial cognitive performance appear to indicate that higher scoring monkeys were more sociable, exploratory, extraordinary, and open.

Table 12

Common Correlated Items across Five Exploratory Factor Structures

Adjective	2	3	4	5	6
Affectionate		+			
Conventional			–	–	–
Cool			–	–	
Curious	+	+	+		
Decisive	+	+			+
Dependent/Follower			–	–	
Depressed	–				
Erratic			+	+	
Excitable	+				
Friendly		+			
Helpful		+			
Independent	+		+	+	
Individualistic	+		+	+	
Innovative	+	+	+	+	+
Inquisitive	+		+		
Intelligent	+	+			+
Inventive	+	+	+	+	+
Persistent	+				+
Playful	+		+		
Quitting	–	–			–
Sensitive		+			
Sociable	+	+			
Stingy/Greedy			+	+	
Sympathetic	+	+			
Thoughtless		–			
Unemotional	–				

Note. Two, three, four, five, and six factor models extracted via Sunho and Lee's Regularized Exploratory Factor Analysis (2011). One factor was significantly correlated with all accuracy measures, and the salient loadings for each such factor are shown. +s indicate positive loadings,–s indicate negative loading. **Bold** adjectives loaded on Openness in the six-component model and *italic* adjectives loaded on Friendliness. The correlated domain of the four factor structure assumed the opposite sign from the other factors, but is consistent with the other loadings, and has been inverted in this table.

Discussion

Rhesus macaques' personalities covary with SimChain task performance: across different measures, Friendliness and Openness were related to performance. These associations extended beyond a priori assumptions about personality structure. Distinct adjectives clustered around factors which consistently correlated with accuracy.

Openness and Friendliness drive distinct aspects of SimChain performance. Friendliness was consistently related to performance over time: the magnitude of asymptotic performance under the Progress metric, and the linear slope of the transformed Error variable, approaching zero (Figure 2). Openness was related to the rate of learning: the steepness of the Progress curve, and the starting point of the Error curve.

The Error models are not clearly interpretable because we needed to model a transformed Error variable in order to cope with Error's inherent non-linearity. Nevertheless, the contributions of Friendliness and Openness are also distinct in these models. The distinction between the effects of different personality dimensions is lost in our models of Rewarded trials and RTs, and considering that the averages of all accuracy measures are very highly correlated, it may be that a single latent variable drives the relationships between performance and both Openness and Friendliness. This is consistent with the observation that the *g* factor predicts performance across diverse mental tasks, while being consistently related to personality (Ackerman & Heggestad, 1997).

Confidence, while not strongly correlated with any performance measure (*r*s = 0.08 to 0.38), repeatedly appeared as a significant predictor, particularly in models of RT. Researchers of general intelligence recognize that external variables, such as speed-accuracy trade-off strategies and assessment anxiety, can affect assessment (Chamorro-Premuzic & Furnham, 2014). Confidence appears to be one such variable, being more closely associated with RTs than accuracy; suggesting that it may play a similar role as Extraversion and Neuroticism, associated with speed-accuracy trading-off and test-taking anxiety respectively, in humans. This is consistent with the fact that Confidence captures situational and social fear (Weiss et al., 2011).

Our results compare favorably to those of Morton et al. (2013), who found correlations between Openness and both task participation and response error in capuchin monkeys. Similarly, chimpanzee participation and performance (Herrelko et al., 2012; Hopper et al., 2014), has been tied to the Openness dimension of that species. However, Morton et al. warn against over-extensive comparisons between studies, as neither personality dimensions nor cognitive tasks tend to be directly analogous to one another. Even if personality dimensions have been assigned the same descriptive names post-hoc, they will never represent quite the same capacities. Similarly, while all cognitive tasks will tap into general and more specific domains of intelligence, for researchers to understand the psychological differences underlying individual and species level differences in performance, task implementation must be as consistent as possible.

While animal studies have only begun to explore the associations between personality and cognitive abilities, the literature on humans is more developed, and ought to be used as one reference point for the formulation of hypotheses and interpretation of results. Openness in humans is modestly to moderately correlated with *g* (Ackerman & Heggestad, 1997), particularly with typical intellectual engagement and crystalized intelligence. Macaque Friendliness does not have a clear analog among the Big Five; it is mostly constituted by adjectives associated with the human domain of Extraversion and Agreeableness, and perhaps crucially, the item 'intelligent', which positively loads on human Openness (DeYoung, 2014). Monkeys scoring high on Friendliness have been described as "sociable and cooperative" (Weiss et al., 2011, p. 77), and it is likely the cooperative aspect of the domain that makes friendly monkeys strong performers.

In humans, RT has been repeatedly correlated with *g* (Jensen, 2006). The fact that correct RTs are predicted by Openness and Friendliness is consistent with a general factor among this species. However, the association between Friendliness and RT is positive (i.e., Friendlier monkeys are slower to respond), in contrast to Openness, which has a negative relationship with RT. Friendliness and Openness mirror each other in predicting accuracy. This divergence is curious, but consistent with the hypothesis that RT and accuracy require different mechanisms (Prinzmetal et al., 2005), and suggests that the mechanism underlying the association between RT and *g* ought to be studied further. RT measures within the human species have proven to be robust, and this study suggests that RT differences could be useful among other primates, but only as a within-species measure. Washburn and Rumbaugh (1997) previously discussed the

comparative flaws in using RT; to grasp the magnitude and significance of cognitive differences between species, researchers must take care when choosing their measures.

Cognitive and neurological evidence indicates that RT and accuracy rely on different architectures (Landau, Esterman, Robertson, Bentin, & Prinzmetal, 2007). What evidence we found reinforces this theory; our results imply that RT can be predicted by personality domains that are not related to accuracy. Our findings strengthen the need for comprehensive, unified testing of primate intelligence, particularly in the context of personality, and we reiterate Morton et al.'s (2013) call for caution when studying animal cognition and personality with small samples.

The Primate Cognition Test Battery (Herrmann et al., 2010) is perhaps the best known collection of cognitive tests for primates, but its assessment of physical and spatial cognition is limited to basic, concrete tests; it contains no test of symbolic reasoning, of which SimChain is but one. The SimChain paradigm has been used in several species (Terrace, 1993; Wagner, Hopper, & Ross, 2015), with immature and adult individuals (Inoue & Matsuzawa, 2009); the task is repeatable and informative. Distinct cognitive tasks are likely to tap into general or domain specific intelligences to varying degrees, and since it is not known how many factors are best for modeling macaque intelligence, it remains an open question which domains SimChain performance draws on. However, even in models of intelligence with more than a general factor, there tends to be significant overlap between specific domains and *g* (Danner, Hagemann, Schankin, Hager, & Funke, 2011). While SimChain is likely representative of *g*, the task is at very least a strong indicator of symbolic reasoning. Additionally, our monkeys had achieved mastery with the SimChain task when tested for this study, so task learning effects would not affect results (Vonk & Povinelli, 2011); this is beneficial since it removes a confound, but it would also be interesting to investigate associations between personality and task acquisition.

More research is needed to determine how tests of serial cognition relate to other tasks, like numerical addition or object transposition (Herrmann et al., 2010). Once relationships between tasks are established, tests of more advanced cognitive faculties could be incorporated into batteries that assess comparable abilities in primates and adult humans. Regardless of whether general intelligence correlates with one of more primate personality dimensions, individual tests - representative of physical, social, or other cognitive proficiencies - might be tied to different personality dimensions, as is suggested in the human literature (Austin et al., 1997; Chamorro-Premuzic & Furnham, 2014). Additionally, factor models of primate intelligence have been investigated (Herrmann et al., 2010; Hopkins et al., 2014), and the results have been favorable.

Complex cognitive tasks, like Raven's Progressive Matrices, are extensively used in human intelligence testing because of their strong associations with general intelligence and specific abilities (Austin et al., 1997). Raven's Matrices is also a difficult task, which is a major reason why it is an effective test (Raven, 2000). Our study demonstrates that nonhuman primates are capable of completing complex cognitive tasks that have meaningful associations with personality and intelligence, and other, difficult tasks need not be ruled out as being too challenging for primates.

Our study is not without limitations. SimChain tests serial cognition, and consequently only assesses a portion of a monkey's cognitive repertoire. For instance, while SimChain allows us to capture characteristics about accuracy, it is not as well-suited for studying RTs – we could only model the latency between stimuli onset and the first response. Our sample of monkeys also contained only males, and while a representative sample ought to of course include females, evidence from multiple tasks showed no sex differences in any performance metrics among a group of six male and seven female long-tailed macaques (Schmitt et al., 2012). However, Hopper et al. (2014) found differing contributions from personality to male and female chimpanzees' problem solving success, so we ought not to rule out the possibility that performance in female macaques may have a different relationship with personality.

A comprehensive study using large samples would be the best way to tackle task consistency, sex differences, and other sources of variability. Different primate species, all of whom have been rigorously trained and tested in a diverse range of cognitive tasks, ought to be rated for personality, which would allow us to address questions concerning the evolution of general and specific types of intelligence, and the common origins of intelligence and personality. Even a broad study such as this would likely suffer

from a drawback that our work suffers from as well: these results rely on captive animals, and captive animals may not be representative of the wider population.

Nevertheless, captive animals are useful models. Rhesus macaques are the gold standard for primate research in neuroscience, genetics, and medicine and our results have implication for these fields. Subjective well-being and personality are heritable and phenotypically and genetically correlated in nonhuman primates (e.g., Adams, King, & Weiss, 2012). Moreover, Friendliness, which is correlated with subjective well-being in macaques (Weiss et al., 2011), is associated with serial intelligence. Subsequent research is needed to determine if the six macaque domains and subjective well-being are heritable, but in humans and chimpanzees, both well-being and personality are heritable, and genetically correlated (Weiss, Bates, & Luciano, 2008; Weiss, King, & Enns, 2002); intelligence too is heritable in both ape species (Davies et al., 2011; Hopkins et al., 2014). The existing monkey literature supports the heritability of personality (Brent et al., 2014; Williamson et al., 2003), though as of yet, no substantive evidence supports the heritability of subjective well-being and intelligence in rhesus macaques. More research needs to investigate these questions, for if individual psychological differences are heritable in macaques, artificial breeding and the research coming out of macaque colonies might be improved by selecting for friendly, intelligent, and mentally healthy phenotypes.

Intelligence and personality are the two pillars of differential psychology. Intelligence has for some time been a major subject of study for evolutionary biologists, and personality has recently gained traction among behavioral ecologists and comparative psychologists (Griffin et al., 2015; Weiss & Altschul, in press). Deeper investigations into primate cognition and personality will enrich both comparative and differential psychology.

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3.2 Personality and cognition, macaques and chimpanzees

This study reports differential effects in the rate at which each individual learned serial lists, and the peak performance of each individual, once a list had been learned. These individual differences in learning and performance were related to personality, most notably, Openness and Friendliness.

Openness was most closely related to the rate of acquisition. High Openness macaques were more likely to have steeper progress curves, indicating faster learning, and lower intercept of the error curves, indicating that fewer mistakes at an early point in the list. Higher Openness individuals also completed entire lists and received rewards more frequently, and displayed faster response times.

Friendliness most closely related to asymptotic accuracy. That is, higher Friendliness subjects, on average, correctly picked a greater number of items in a list, after the individual had learned a given list and performance had stabilized. It ought to be noted that in these macaques, learning a list did not confer perfect accuracy, but as mentioned, performance was visibly asymptotic. Friendliness was also negatively associated with error as the subjects gained experience; higher Friendliness individuals were more successful at completing full trials, as well. However, higher Friendliness individuals took significantly longer to make responses.

Friendliness does not have a direct analogue in chimpanzee or human personality. Friendliness is a mix of items which load on chimpanzee Agreeableness and Extraversion (King & Figueredo, 1997; Weiss, Inoue-Murayama, et al., 2009), plus three items from chimpanzee Dominance: ‘intelligent’, ‘persistent’, and

'decisive'. If one considers where the items load on human personality dimensions, Agreeableness is the most strongly represented (6 items), but Friendliness also draws from 3 items from human Extraversion, 2 from Conscientiousness, and 1 from Openness (Weiss, Adams, Widdig, et al., 2011). It was difficult to make predictions for what relationship might exist between Friendliness and performance. Overall, the association was positive. Given the links to Extraversion, we might expect high Friendliness macaques to have faster response times, but the effect we found was the opposite of this.

As mentioned, these data represent expert subjects: macaques that were performing at the peak of their abilities. Our results suggest that previous associations between performance and personality dimensions like Openness are not solely the result of greater interest in the tasks on the part of high Openness individuals – our results showed a positive association between performance and Openness even though the macaques performed this task as part of their daily regimen and were not learning anything new about how the task functioned.

On the other hand, the context in which the macaques performed this task can and should be viewed in an alternative light: these were expert subjects, thus the learning capabilities described should not be extrapolated to task acquisition. This sample was already the subject of some selection bias, as more behaviorally difficult macaques are not often used in research that requires the macaques be extensively trained. Naïve macaques at a breeding colony, for example, might display different associations between personality and how quickly they completed basic training tasks.

Rhesus macaques do not have a dimension of personality that is easily comparable to Conscientiousness. The adjective items that constitute chimpanzee Conscientiousness are evenly spread across the dimensions of macaque personality, with the exception of Friendliness, which has none. Yet, Friendliness is loaded with two items of human Conscientiousness, 'persistent' and 'decisive', both of which are among the strongest of the Friendliness items correlated with performance in the sensitivity analysis. Macaque Openness contains 'thoughtless' and 'impulsive', two chimpanzee Conscientiousness items, which in our sensitivity analyses were not major contributors to predicting performance. It may be that Conscientiousness, though not strong enough to form a distinct dimension in rhesus macaques, does play a role in performance via Friendliness. A longitudinal regimen of training and testing, like that conducted in chapter 2, would likely elucidate any additional role that Friendliness or Openness might play in learning.

It is also difficult to disentangle serial cognitive ability from test performance, or rather, it is possible that the best performing individuals might have the most favorable personality types for spending time in the experimental chambers. If this were the case, we would have expected that the Anxiety dimension of macaque personality would have been implicated in performance, and items like 'persistent', 'cool', and 'quitting' would have been more influential. These items were important in our factor analyses, but not as important as items like 'inventive' and 'innovative', which are less obviously linked to how well an individual might have adjusted to working in the experimental chambers. However, with this limited set of data, no firm conclusion can be reached.

Sample size is an issue for this study, though we took steps to verify our findings. As demonstrated in chapter 2, including many trials per individual can help alleviate the issues of insufficient power in small sample sizes. We gathered 800 trials with each macaque in this study, which was comparable to the number of trials we gathered per individual in studies 1 and 2 of chapter 2. We analysed and reported several measures to avoid falling prey to isolated false-positives. In all models and in a sensitivity analysis, the results were remarkably similar.

Chapters 2 and 3 present results that are in many ways complementary, but the direct comparison of differential psychological results from different species is problematic (Morton, Lee, & Buchanan-Smith, 2013). Careful, consistent test and test battery design will be crucial to the success of future research in comparative differential psychology.

Test batteries ought to clearly target a wide range of domains, and if there are logistical limitations that prevent this, then single domains ought to be targeted, as using fewer, more similar tasks makes individual projects more achievable (Shaw & Schmelz, 2017). As the time of writing, test batteries have tended to focus on overall cognitive ability, and the study lower order domain abilities, such as serial cognition, has been neglected. Regardless of whether or not a general factor of intelligence is present in some, most, or even all animal species, understanding the hierarchical structure of intelligence is crucial to understanding how cognition evolved.

Good test batteries alone are not enough, however. Researchers must ensure that their samples are large enough, and also diverse enough. Non-cognitive factors, such as prior experience and personality, can introduce biases that will distort finding

on cognitive ability, as demonstrated in chapter 2 and elsewhere (Morton, Lee, & Buchanan-Smith, 2013). Some of these biases can be reduced through good test battery design, but bias reduction approaches must also consider the testing environment, e.g. whether animals feel comfortable and safe, and will not be distracted. In general, identifying and measuring non-cognitive variables will allow researchers to adjust for these effects, both experimentally and analytically.

At the time of writing, phylogenetic statistical approaches that allow for direct comparison between species are becoming viable (MacLean et al., 2014; MacLean et al., 2012), much of what we lack is sufficient data. Chapters 2 and 3, when viewed in the context of the literature, suggest that there are consistent associations between personality and cognitive abilities across primate species. To understand the evolutionary underpinnings of differential psychology, we need to explore these associations in more species.

This document now turns to the psychosomatic correlates of primate personality. Chapters 4 through 6 will investigate the associations between chimpanzee personality, health and longevity.

4 Personality and longevity in captive chimpanzees

4.1 Introduction

As organisms age, mortality risk increases due to the gradual deterioration of vital functions. This accumulation of harmful effects in an aging organism, known as biological senescence, impacts fitness as it makes organisms more likely to die from predation, disease, or natural causes (Williams, 1957), and, consequently, in insects (James & Warren, 1991), birds (Newton, 1989), and mammals (Kjellander, Gaillard, Hewison, & Liberg, 2004; Silk et al., 2010), leave fewer surviving offspring.

Converging evidence from studies of Old World monkeys, great apes, and humans, show that several aspects of individuals' social lives are linked to survival and possible proxies of survival, such as allostatic load and inflammation (Uchino, Cacioppo, & Kiecolt-Glaser, 1996). For instance, the social standing of a monkey, ape, or human affects physiological stress responses (Sapolsky, 2005). Among male olive baboons, submissive, isolated individuals have higher levels of cortisol, suggesting increased allostatic load (Virgin & Sapolsky, 1997). In chimpanzees, high-ranking individuals are generally less stressed, but when the hierarchy is destabilized, for example, when a coalition of low-ranking males challenge a high-ranking male in order to advance in social rank, the high-ranking individual becomes more stressed; instability and reorganization can be common in wild chimpanzee groups (Mitani et al., 2002; Sapolsky, 2005). Additionally, rhesus macaque immune function and gene expression is known to respond to changes in social status

(Snyder-Mackler et al., 2016), and in humans, chronic stress associated with low socioeconomic status has wide-ranging, consistent negative effects on health and longevity (Eikemo et al., 2014).

The strength of social bonds is also associated with survival and fitness. For example, the overall level of affiliative interaction among female savannah baboons is associated with survival (Silk et al., 2010). Similar associations between sociability and survival have been found for the closeness of bonds between male Assamese macaques (Schülke, Bhagavatula, Vigilant, & Ostner, 2010), high network centrality within coalitions among male chimpanzees (Gilby et al., 2013), and for social relationship strength in humans (Holt-Lunstad, Smith, & Layton, 2010).

Differences in the quantity, quality, and hierarchical asymmetry of social interactions, which affect survival, are expressions of personality differences. For example, female chacma baboons characterized as nice or aloof retained a stable set of social partners over several years, and nice baboons demonstrated higher overall sociality (Seyfarth et al., 2012); both higher social stability and sociality are linked to survival (Silk et al., 2010). Moreover, western lowland gorillas higher in Extraversion, i.e., gorillas that were more sociable, playful, active, popular, and curious, and less solitary and slow (Kuhar, Stoinski, Lukas, & Maple, 2006), were more likely to still be alive nearly 19 years later in comparison to individuals that were rated lower in Extraversion (Weiss et al., 2013).

The personality traits and other individual differences that affect survival in nonhuman primates and humans extend beyond traits that reflect one's place in a social hierarchy or one's behavior in the social world. Personality traits related to

self-control, exploration, emotional reactivity, and vigilance are also related to survival. Across a variety of nonhuman animal species, including primates, individuals lower in boldness and higher in exploratory behavior and aggressiveness in novel environments, survived longer (Smith & Blumstein, 2008).

Personality traits are also associated with survival in humans. These studies typically use a set of five personality dimensions, known as the "Big Five" or "Five-Factor Model" (Digman, 1990). These dimensions include social traits (Extraversion and Agreeableness) like those described in the previous paragraph, but also traits related to self-control (Conscientiousness), exploration (Openness to experience), and emotional reactivity and vigilance (Neuroticism). However, personality dimensions related to social standing have not been identified in human personality models (Digman, 1990). Broadly speaking, Extraversion and Agreeableness characterize how often and how well we navigate our social world, respectively (Leary & Hoyle, 2009). Although aspects of Extraversion, namely positive emotions, are associated with survival (Roberts et al., 2007), the association between survival and Agreeableness is more consistent and robust (Strickhouser et al., 2017).

Some of the remaining non-social traits are also associated with longer life in humans. Higher Conscientiousness, reflecting self-control and persistence, is most commonly and usually most strongly associated with increased longevity (Jokela et al., 2013; Roberts et al., 2007). Higher Neuroticism, reflecting higher reactivity, is often associated with decreased longevity (Roberts et al., 2007). However, Openness, which reflects exploratory behavior, does not appear to have a consistent or strong

association with longevity (Turiano, Spiro III, & Mroczek, 2012; Weiss & Costa, 2005) or general health (Strickhouser et al., 2017).

Social rank is most often operationalized through socioeconomic status (SES) in humans (Sapolsky, 2004); while low SES is associated with reduced longevity (Eikemo et al., 2014; Lynch, Smith, Kaplan, & House, 2000), the effect size of SES is less than the effect size imparted by personality (Roberts et al., 2007). Broadly speaking, rank, dominance, or SES can often have an effect on longevity and health, but species or even population specific circumstances can moderate or eliminate these effects (Sapolsky, 2004).

Chimpanzees and humans share a recent common ancestor, and thus studying chimpanzees enables us to identify behaviors present in our common ancestor. This research has found, for example, that culture and intragroup aggression are not characteristics exclusive to modern humans (Whiten et al., 1999; Wilson et al., 2014). Similar studies found that chimpanzees possess five personality dimensions like those of humans, plus a dimension termed Dominance (Freeman & Gosling, 2010) that reflects competitive prowess, social competence, and fearlessness (King & Figueredo, 1997).

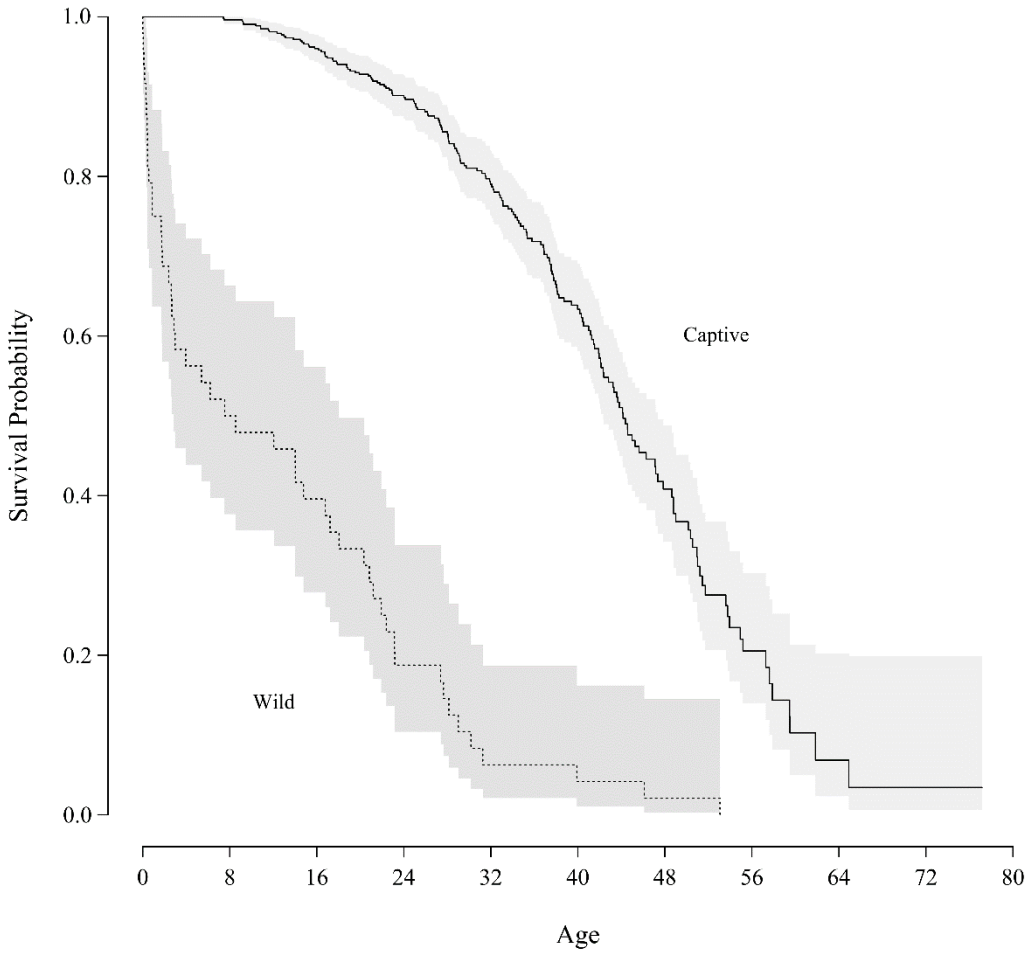
The question, then, is whether associations between human personality traits and longevity were present in our common ancestor or whether they reflect modern, and perhaps ancestral, humans' ability to have some control over their health, e.g., by exercising voluntarily, or taking steps to eliminate health threats, such as smoking? To these ends, we studied associations between personality traits and mortality, assessed during a 6 to 23 year follow-up period, in a large, comprehensive sample of

chimpanzees living in zoological parks, research facilities, and sanctuaries located in the United States, the United Kingdom, Australia, and Japan.

A Kaplan-Meier plot (Figure 4.1) shows the survival functions for our captive chimpanzees, as well a wild sample. Unlike wild chimpanzees, where many individuals die when they are young (Bronikowski et al., 2011), in this population, individuals survive longer with mortality accelerating in older ages. Similar observations have been used to argue that captive chimpanzee populations have undergone a demographic transition (Hawkes, Smith, & Robson, 2009), such as human populations have undergone in the post-industrial age.

Figure 4.1

Survival curves of captive and wild chimpanzees.



Note. Lines indicate survival probability of each group over the lifespan. The solid lines represent the captive population used in this study, and the dashed line corresponds to a wild group (Bronikowski et al., 2016). The shaded areas indicated the 95% confidence region for reach group.

This study benefits from the fact that captive chimpanzees receive good health care, plenty of food, and are protected from the elements and predators, including humans. As such, captive environments resemble modern, affluent human societies, rather than the environments of wild nonhuman primates. If the personalities of captive chimpanzees are associated with longevity, as they are in humans, we would

expect to find that chimpanzees higher in Agreeableness, Conscientiousness, and lower in Neuroticism would live longer (Strickhouser et al., 2017). These findings would strongly suggest that the associations between survival and these personality dimensions in humans are not just mediated by health-related behaviors (Turiano, Chapman, Gruenewald, & Mroczek, 2015), but also reflect deeper biological causes. If, however, the personality-mortality association in chimpanzees follows the patterns found in other nonhuman primates, we would expect to find that Dominance and Extraversion are related to longer life. This finding would also be consistent with the personality-survival association in humans being derived and/or attributable to the consequences of certain behaviors in modern human societies.

4.2 Methods

4.2.1 Sample

556 chimpanzees were assessed for personality between 1993 and 2010. Eighteen chimpanzees had to be removed from the sample due to incompatibilities with the study design (e.g., personality was assessed after death). Of the 538 remaining chimpanzees, 175 came from American zoos, 164 came from the Yerkes National Primate Research Center (USA), 156 came from zoos, a sanctuary, and a research centre in Japan, 21 came from the Taronga Zoo in Australia, and 22 came from the Edinburgh Zoo (UK).

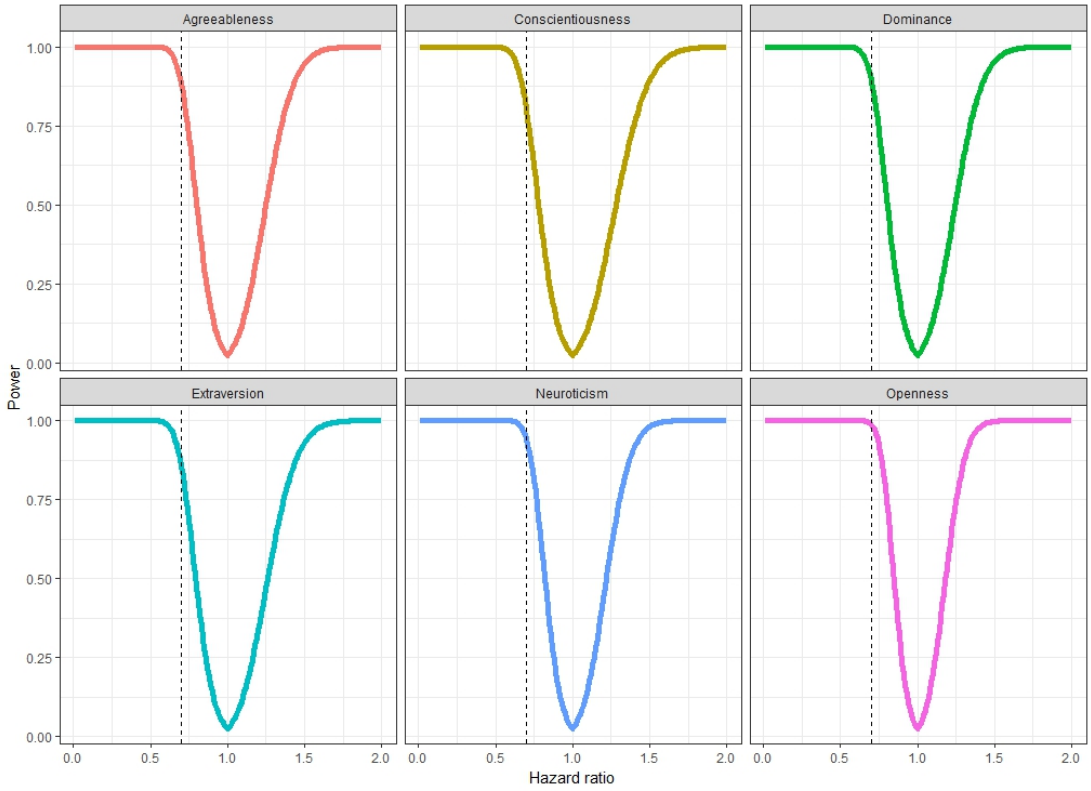
Vital status was recorded throughout 2016, yielding follow-up times ranging from 6 to 23 years, approximately equivalent of 9 to 35 human years (Napier & Napier, 1967). A total of 187 chimpanzees died during the follow-up period. Our analytic approach treated the remaining 353 chimpanzees as right-censored at the

date that mortality data were gathered for that group. Individuals who were lost to follow were censored at the last date of record known for each individual. All records were also left-truncated, beginning each record at the age at which the individual was assessed for personality.

We evaluated power using a range of effect sizes, and created power curves (Figure 4.2). A similar study of gorillas found single significant effect of Extraversion on longevity (Weiss et al., 2013); the hazard ratio for the effect was 0.688. Informed by these findings, we selected a conservative estimate of effect size: 0.7. For a hazard ratio of 0.7, the mean power to detect the effect of any personality dimension in our sample was 0.88 (range: 0.80 to 0.98).

Figure 4.2

Power curves for survival analyses.



Note. The power to detect the effects of each personality dimension, across a range of hazard ratios. The dashed lines indicate our best estimate of hazard ratio (0.7).

4.2.2 Personality assessments

Fifty-four items comprising a trait name, e.g., “Fearful” and a one to three sentence behavioral description, e.g., “Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.” were developed to assess the personalities of the chimpanzees (King & Figueredo, 1997; Weiss, Inoue-Murayama, et al., 2009). Between 1993 and 2005, 43 of these items were used to assess the personalities of chimpanzees in the American Zoos (King & Figueredo, 1997), the Taronga Zoo

(King & Figueredo, 1997), and chimpanzees living at the Yerkes National Primate Research Center (Weiss et al., 2007). Starting in 2007, all 54 items were used to assess the personality of the chimpanzees living in Japan (Weiss, Inoue-Murayama, et al., 2009) and at the Edinburgh Zoo (Herrelko et al., 2012).

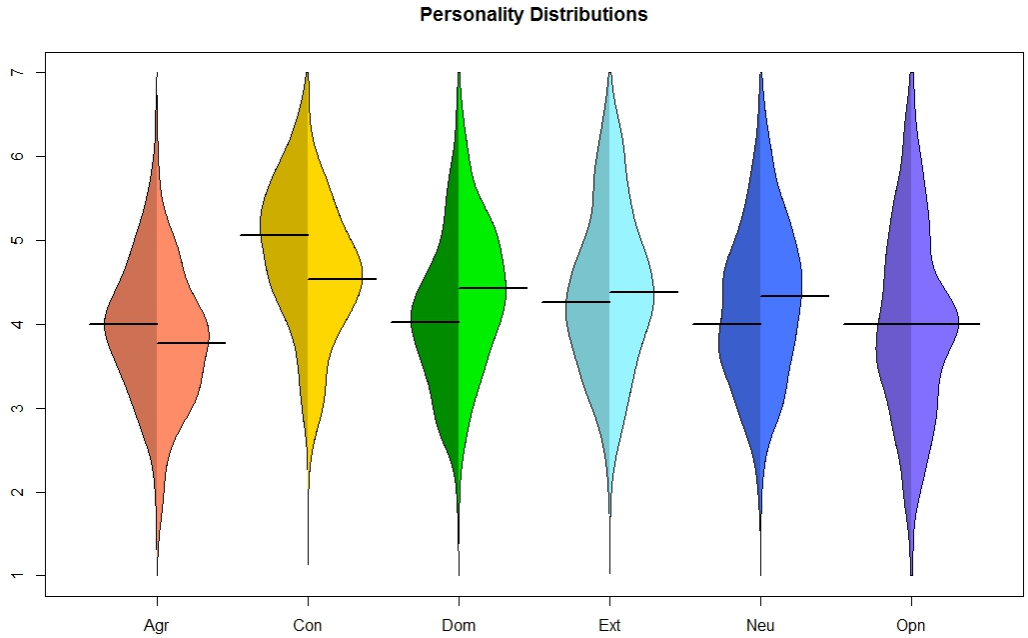
The personalities of the chimpanzees in this study were assessed via ratings on questionnaires by multiple keepers and researchers who knew the individual chimpanzees, sometimes for decades (Weiss, Inoue-Murayama, et al., 2009; Weiss et al., 2007). In addition to showing that the interrater reliabilities are comparable to those found in human studies of personality, previous studies have shown that chimpanzee personality, measured this way, yields measures that are more reliable than behavioral codings (Vazire, Gosling, Dickey, & Schapiro, 2007), heritable (Latzman, Freeman, Schapiro, & Hopkins, 2015; Weiss, King, & Figueredo, 2000; Wilson et al., 2017), stable over time (King et al., 2008), and that generalize across samples (King, Weiss, & Farmer, 2005; Weiss, Inoue-Murayama, et al., 2009; Weiss et al., 2007), and are not adversely affected by anthropomorphic attributions on the part of the raters (Weiss et al., 2012). Finally, these measures have been related to observed behaviors (Pederson, King, & Landau, 2005), the brain (Blatchley & Hopkins, 2010; Latzman, Hecht, Freeman, Schapiro, & Hopkins, 2015), and genetic polymorphisms (Hong et al., 2011; Hopkins, Donaldson, & Young, 2012; Wilson et al., 2017). Beanplots of all six personality dimensions are shown in Figure 4.3. Each personality dimension was scaled and centered for all analyses.

Chimpanzee personality is known to change over time (King et al., 2008; Weiss & King, 2015) and these effects could bias the results of our analyses. For

example, chimpanzees who are older tend to have lower Extraversion. In an analysis which uses data from individuals rated at the same point in life, this should not be an issue, but our data were taken from individuals across the lifespan. So in this example, an analysis might spuriously associate low Extraversion with longer life because it happens that aging is also associated with a lowering of Extraversion. These two processes are not easily disentangled, but we can adjust confounded personality covariates if we understand their relationship with age. Our sample includes individuals at every stage of life, so we could model these associations and extract age-adjusted covariates for later analysis. These analyses are presented in section 4.3.1, and the resultant adjusted personality domains are used in 4.3.2, though always alongside the original unadjusted personality data.

Figure 4.3

Beanplots for all chimpanzee personality dimensions.



Note. Agr = Agreeableness, Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Neu = Neuroticism, Opn = Openness. The left side of each bean plots the data from females, the right side plots the data from males.

4.2.3 Survival Analyses

To be conservative, our survival models included all six personality scores. We also included sex and origin (whether the individual was born in the wild or not) as controls.

We used decision-tree analyses to identify associations between personality and longevity. Parametric and semi-parametric survival regression models force a specific link between variables and outcome, but decision trees do not impose any such assumptions; without supervision, trees are able to identify meaningful

variables and even some interactions without prior specification (Bou-Hamad, Larocque, & Ben-Ameur, 2011). As our power analyses indicated, we had good power (greater than 0.8) to detect effects on this scale, however, we needed to be able to include many variables in our analyses, and many possible linking distributions could be used. In order to reduce multiple testing, we preferred decision-tree analyses as they do not require parameterization and are able to identify potential interactions.

Survival trees have other advantages over traditional techniques. In simulation studies of left-truncated right-censored decision trees with data much like ours, i.e., a large sample with ($N > 500$) many censored observations (> 50%), relative risk and conditional inference trees identified the correct predictors 94% and 93% of the time, respectively (Fu & Simonoff, 2016). These methods can handle binary and continuous variables, and are robust to the effects of time-dependent covariates, e.g., several of our chimpanzees' personality dimensions.

Nevertheless, to maintain a balanced, conservative approach, we grew trees with both unadjusted and adjusted covariates, as indicated by the previous section. Adjusted covariates were residualized versions drawn from the linear or quadratic regression models fitted to model the effects of age on personality (see section 4.3). Using adjusted covariates had no effect on the growth of our trees; they did not grow past the inclusion of Agreeableness (which was unconfounded by time) with either set of variables, thus the outputs of our tree analyses were identical.

We validated our decision-tree analyses with multiple fully parametric hazard regression models. Again, to reduce risks brought on my multiple testing, we did not

analyse individual models, but rather, followed an information theoretical approach which allowed us to pool and average model estimates across a wide-range of possible choices of error distribution and variables to include (Burnham, Anderson, & Huyvaert, 2011). For example, one could specify a model for which there are two possible variables (A & B) to include, and two reasonable error distributions (C & D). The variables are not mutually exclusive, so there are three possible variable specifications: only A, only B, and A + B. Error distributions are mutually exclusive, so there are only two options, C or D. In this example, there are thus six specifications that combine all possibilities.

The information theoretical approach starts weighting each model based on its fit, as assessed by the Akaike Information Criteria (AIC). The weighting will give more influence in the overall aggregated model to models with better fit. To continue our example, if variable A happens to have a true relationship with the outcome variable, and error distribution C happens to accurately capture the outcome's distribution, then specifications featuring A will have a higher weight, specifications modelling with C will have a higher weight, and specifications which use both A and C will have still higher weights. In this way, the estimates and confidence intervals of coefficients within each aggregated model are meaningfully informed by many specifications, producing more robust, interpretable results (Wagenmakers & Farrell, 2004).

We first built two sets of models, again, with unadjusted covariates and without adjusted covariates. Adjustment creates a different, alternative dataset which cannot be directly compared to the unadjusted data, so our evaluations of these

models were necessarily kept separate. The linking distributions we used included the Weibull, Gompertz (Klein & Moeschberger, 2005), exponential piecewise-equidistant and piecewise percentile (Goodman, Li, & Tiwari, 2011) survival functions. The parametric hazard models were also fit with Gamma (except where noted) distributed frailty (random) effects, to control for any influence that the different sample groups might have on survival. We also built models including and excluding the demographic covariates of sex and origin.

4.3 Results

4.3.1 Relationships between age and personality

Inspection of the six chimpanzee personality dimensions (Figure 4.4), as well as prior studies (King et al., 2008), indicated that personalities changed as individuals aged, making it possible that an association between personality and longer life might be confounded. To determine whether any personality dimension was so-confounded, we tested for associations between date of birth and each personality dimension. The Kendall tau-b correlations between date of birth and Dominance (τ = -0.15, $p < 0.001$), Extraversion ($\tau = 0.35$, $p < 0.001$), Neuroticism ($\tau = 0.09$, $p < 0.036$), and Openness ($\tau = 0.25$, $p < 0.001$), but neither Conscientiousness (τ = -0.07, $p < 0.12$) nor Agreeableness (τ = -0.08, $p < 0.077$), were significant.

Figure 4.4

Scatterplots of age and measurements of each personality dimension.

Note. The personality score of each individual, across all six dimensions of chimpanzee personality. Dominance, Extraversion, Neuroticism, and Openness all change over the course of the lifespan.

Again, to be conservative, we modelled, and therefore controlled for, these potential confounds between time and personality dimensions. We fitted three models each for Dominance, Extraversion, Neuroticism, and Openness, predicting the personality dimension from date of birth. The first model included only an intercept, the second added a linear component of date of birth, and the third added a quadratic component of date of birth. Our models indicated that a quadratic model

was the best fit for Dominance, Extraversion, and Openness, and a linear model was the best fit for Neuroticism (Table 4.1).

Table 4.1

Models of change in personality with age.

	Dominance		Extraversion		Neuroticism		Openness	
Model	LL	AIC	LL	AIC	LL	AIC	LL	AIC
Intercept only	-763.7	1531.3	-755.8	1515.5	-756.2	1516.4	-760.2	1524.4
Linear	-754.1	1514.2	-681.4	1368.8	**-751.2**	**1511.3**	-734.9	1475.8
Quadratic	**-750.5**	**1509.0**	**-668.7**	**1345.5**	-752.6	1513.3	**-725.7**	**1459.4**
Cubic	-750.2	1510.5	-668.3	1346.8	-751.2	1512.6	-725.2	1460.4

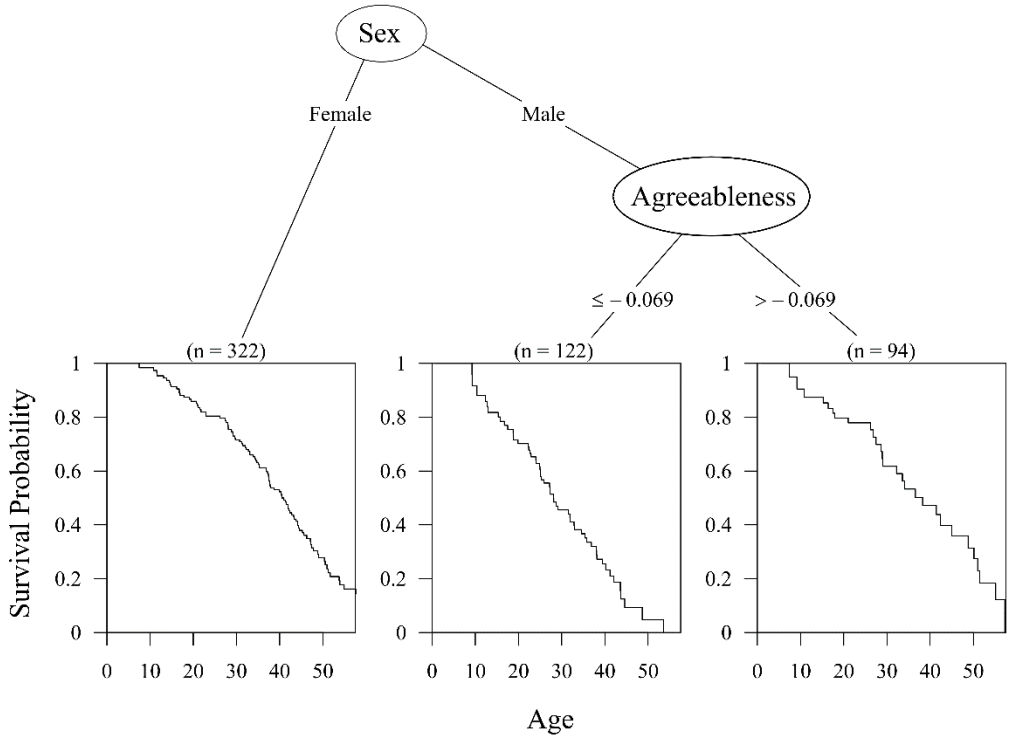
Note. LL = log-likelihood, AIC = Akaike Information Criterion. The best fit model for each dimension, chosen by incremental likelihood ratio testing, are shown in bold.

4.3.2 Relationships between personality and longevity

We fit decision tree models to test whether sex, origin, or any personality dimensions were related to longevity. A relative risk survival tree indicated that the dimension of Agreeableness was associated with survival. More than half of the individuals with Agreeableness scores lower than 1.3 standard deviations below the mean (23 out of 45) had died, whereas individuals above this threshold faced a reduced risk of mortality (164 out of 493). An extension of the relative risk tree analysis, which applied conditional inference to the tree, demonstrated that the effect was more pronounced in males than in females (Figure 4.5). Specifically, males with Agreeableness scores less than 0.069 standard deviations below the mean were at significantly higher risk than other males ($p < 0.024$).

Figure 4.5

Conditional inference tree diagram indicating variables influencing survival.



Note. Bottom panes indicate the survival curves of and number of chimpanzees in each sub-group. Sub-groups were split based on the growth of the tree, and decision criteria are indicated below each node.

In our parametric hazards models we found the expected significant effect of sex – females live longer than males (Table 4.2). We also found a notable, but non-significant effect of Agreeableness. The full set of models is used to calculate averaged estimates and confidence intervals is shown in Table 4.3.

Table 4.2

Survival model estimates of personality and demographic variables related to longevity.

	Unadjusted			Adjusted for date of birth		
Variable	Hazard Ratio	95%	C.I.	Hazard Ratio	95%	C.I.
Sex	1.58	[1.15,	2.19]	1.60	[1.16,	2.21]
Wild-born	1.29	[0.89,	1.85]	1.28	[0.89,	1.83]
Agreeableness	0.84	[0.67,	1.04]	0.82	[0.67,	1.02]
Dominance	1.07	[0.90,	1.27]	1.05	[0.88,	1.25]
Extraversion	1.17	[0.91,	1.50]	1.18	[0.91,	1.52]
Conscientiousness	1.10	[0.89,	1.37]	1.09	[0.88,	1.35]
Neuroticism	0.99	[0.83,	1.19]	0.97	[0.81,	0.17]
Openness	0.85	[0.70,	1.04]	0.87	[0.71,	1.07]

Note. Estimates and confidence intervals are computed as weighted averages from the set of models in Table 4.3.

Table 4.3

Individual regression estimates and information criteria for whole sample models used in weighted averages.

	Wild-born	Sex	Agr	Dom	Ext	Con	Neu	Opn	*K*	Δ*AIC*	Weight
Unadjusted											
Weibull	0.32	0.48	-0.18	0.01	0.18	0.10	-0.02	-0.13	11	7.61	0.01
	0.33		-0.18	0.08	0.21	0.08	0.00	-0.20	10	8.18	0.01
		0.46	-0.16	0.06	0.13	0.13	0.00	-0.13	10	3.61	0.08
			-0.16	0.11	0.19	0.09	0.01	-0.19	9	9.39	0.00
Piecewise-equidistant	0.36	0.43	-0.11	0.09	0.10	0.13	0.04	-0.21	12	24.67	0.00
	0.39		-0.12	0.13	0.16	0.09	0.05	-0.26	11	29.49	0.00
		0.45	-0.08	0.12	0.06	0.14	0.05	-0.20	11	26.35	0.00
			-0.09	0.16	0.12	0.11	0.06	-0.25	10	31.86	0.00
Piecewise-percent	0.23	0.45	-0.13	0.09	0.12	0.11	0.04	-0.20	12	21.40	0.00
	0.27		-0.13	0.13	0.17	0.08	0.04	-0.26	11	26.81	0.00
		0.47	-0.11	0.10	0.10	0.12	0.04	-0.19	11	20.74	0.00
			-0.11	0.15	0.15	0.08	0.05	-0.25	10	26.85	0.00
Gompertz	0.24	0.45	-0.19	0.06	0.16	0.10	-0.01	-0.16	11	0.36	0.39
	0.29		-0.19	0.10	0.22	0.06	0.00	-0.22	10	5.73	0.03
		0.47	-0.17	0.08	0.15	0.10	-0.01	-0.15	10	0.00	0.46
			-0.17	0.12	0.21	0.07	0.00	-0.21	9	6.10	0.02
Adjusted											
Weibull	0.30	0.49	-0.16	0.01	0.14	0.09	-0.02	-0.12	11	7.60	0.01
	0.33		-0.17	0.06	0.21	0.06	-0.01	-0.19	10	14.31	0.00
		0.50	-0.15	0.03	0.15	0.10	-0.02	-0.11	10	8.27	0.01
			-0.17	0.10	0.20	0.09	0.00	-0.18	9	8.96	0.01
Piecewise-equidistant	0.37	0.44	-0.15	0.05	0.17	0.11	0.02	-0.19	12	24.96	0.00
	0.40		-0.16	0.09	0.22	0.08	0.03	-0.24	11	30.01	0.00
		0.45	-0.12	0.08	0.15	0.13	0.03	-0.18	11	27.01	0.00
			-0.13	0.12	0.21	0.09	0.04	-0.23	10	32.64	0.00

Piecewise-percent	0.23	0.46	-0.15	0.05	0.16	0.10	0.02	-0.17	12	21.66	0.00
	0.27		-0.16	0.10	0.22	0.06	0.03	-0.24	11	27.38	0.00
		0.47	-0.14	0.07	0.15	0.11	0.02	-0.17	11	21.06	0.00
			-0.15	0.11	0.22	0.07	0.03	-0.23	10	27.43	0.00
Gompertz	0.24	0.46	-0.19	0.04	0.16	0.08	-0.03	-0.13	11	0.42	0.42
	0.28		-0.20	0.09	0.15	0.05	-0.02	-0.20	10	6.15	0.02
		0.48	-0.18	0.05	0.16	0.09	-0.03	-0.13	10	0.00	0.51
			-0.19	0.10	0.22	0.05	-0.02	-0.19	9	6.44	0.02

Note. Agr = Agreeableness, Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Neu = Neuroticism, Opn = Openness, K = numbers of parameters in the model, AIC = Akaike Information Criterion. Weightings for wild-born and sex estimates do not include all models, thus their weights differ slightly but not substantially, and are not shown. As a binary variable, a 1 for sex indicates a male.

Because our conditional inference tree suggested that the effect of Agreeableness was especially pronounced among males, we split our sample by sex, and re-fit our regression models. These models confirmed that the protective effect of Agreeableness does exist in males; the effect in females goes in the opposite direction (Table 4.4). However, we did find a protective effect of Openness in female chimpanzees only. These effects were consistent across all constituent models, the estimates of which can be seen in Table 4.5.

Table 4.4

Survival model estimates of personality and demographic variables related to longevity.

	Unadjusted			Adjusted for date of birth		
Variable	Hazard Ratio	95%	C.I.	Hazard Ratio	95%	C.I.
Male (n = 216)						
Wild-born	1.41	[0.69,	2.90]	1.39	[0.69,	2.81]
Agreeableness	0.66	[0.47,	0.89]	0.65	[0.48,	0.89]
Dominance	0.98	[0.74,	1.29]	0.97	[0.73,	1.28]
Extraversion	1.04	[0.71,	1.52]	1.02	[0.67,	1.53]
Conscientiousness	1.12	[0.78,	1.60]	1.11	[0.78,	1.58]
Neuroticism	0.91	[0.66,	1.26]	0.89	[0.65,	1.24]
Openness	1.09	[0.76,	1.56]	1.12	[0.78,	1.61]
Female (n = 322)						
Wild-born	1.20	[0.75,	1.91]	1.20	[0.75,	1.92]
Agreeableness	1.10	[0.82,	1.48]	1.09	[0.81,	1.46]
Dominance	1.05	[0.84,	1.31]	1.02	[0.81,	1.28]
Extraversion	1.17	[0.81,	1.71]	1.19	[0.82,	1.72]
Conscientiousness	1.00	[0.75,	1.34]	0.99	[0.74,	1.33]
Neuroticism	0.92	[0.72,	1.17]	0.91	[0.71,	1.16]
Openness	0.75	[0.59,	0.97]	0.77	[0.60,	0.99]

Note. Values are model averaged parameter estimates and unconditional confidence intervals calculated from weighted estimates shown in Table 4.5

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Table 4.5

Individual regression estimates and information criteria for sex split models used in weighted averages.

	Wild-born	Agr	Dom	Ext	Con	Neu	Opn	*K*	Δ*AIC*	Weight
Male										
Unadjusted										
Weibull	0.46	-0.42	-0.07	0.06	0.10	-0.11	0.09	10	2.59	0.13
		-0.39	0.00	0.04	0.13	-0.09	0.06	9	2.65	0.13
Piecewise	0.31	-0.44	0.03	-0.05	0.20	-0.03	0.12	11	8.62	0.01
		-0.41	0.08	-0.06	0.21	-0.01	0.10	10	7.40	0.01
Gompertz	0.26	-0.43	-0.01	0.04	0.10	-0.10	0.10	10	1.46	0.23
		-0.42	-0.01	0.03	0.11	-0.09	0.08	9	0.00	0.49
Adjusted										
Weibull	0.46	-0.43	-0.08	0.05	0.10	-0.12	0.11	10	2.66	0.13
		-0.40	-0.03	0.06	0.11	-0.11	0.08	9	3.22	0.10
Piecewise	0.34	-0.44	0.01	-0.07	0.18	-0.05	0.16	11	8.53	0.01
		-0.42	0.05	-0.06	0.20	-0.04	0.13	10	7.49	0.01
Gompertz	0.26	-0.43	-0.05	0.01	0.10	-0.12	0.13	10	1.46	0.24
		-0.43	-0.02	0.02	0.11	-0.11	0.11	9	0.00	0.50
Female										
Unadjusted										
Weibull	-0.09	-0.22	-0.06	0.69	0.01	-0.15	-0.22	10	106.23†	0.00
		-0.19	0.03	0.12	0.02	-0.07	-0.24	9	108.08†	0.00
Piecewise	0.17	0.14	0.08	0.14	0.00	-0.03	-0.35	11	16.69	0.00
		0.16	0.08	0.12	0.00	-0.03	-0.34	10	15.15	0.00
Gompertz	0.18	0.09	0.05	0.17	0.00	-0.08	-0.29	10	1.45	0.33

		0.10	0.05	0.16	0.00	-0.08	-0.28	9	0.00	0.67
Adjusted										
Weibull	0.18	0.11	0.04	0.11	0.02	-0.07	-0.25	10	2.29	0.17
		0.10	0.03	0.16	0.02	-0.08	-0.20	9	8.77	0.01
Piecewise	0.17	0.09	0.01	0.23	-0.02	-0.07	-0.31	11	17.80	0.00
		0.10	0.01	0.22	-0.02	-0.07	-0.29	10	16.26	0.00
Gompertz	0.18	0.07	0.02	0.19	-0.01	-0.10	-0.27	10	1.43	0.27
		0.08	0.02	0.19	-0.01	-0.11	-0.25	9	0.00	0.55

Note. Agr = Agreeableness, Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Neu = Neuroticism, Opn = Openness, K = numbers of parameters in the model, AIC = Akaike Information Criterion. Weightings for wild-born and sex estimates do not include all models, thus their weights differ slightly but not substantially, and are not shown. As a binary variable, a 1 for sex indicates a male. † indicates models for which frailty could not be estimate with the Gamma distribution; the Log-Normal distribution was used instead.

4.4 Discussion

In this study of captive chimpanzees, we found clear connections between personality and longevity, but generally not those we expected. Despite social standings being implicated in stress and health in many primate species (Sapolsky, 2005), we found no effect of Dominance on longevity in captive chimpanzees. Dominance may not play a major role in influencing longevity in captive populations because fission-fusion dynamics are not as influential, thus group stability will be greater, and stressful disruption less of a concern. Moreover, in captivity there is less need to contest with other chimpanzees for resources; ultimately, all individuals will be sufficiently fed and otherwise provided for in captivity, except in extreme circumstances. Thus, traits such as Dominance, which are related to rank, would have less of an impact in this regard as well.

Among the domains of personality which chimpanzees and humans share, we were surprised to find no association between Extraversion and longevity. Studies in humans (Roberts et al., 2007) and other primates (Seyfarth et al., 2012; Silk et al., 2010) have shown positive, protective effects of high sociality. Of particular note, a positive effect was found in similar a study of gorillas, which were also kept in captivity, and assessed for personality by means of ratings (Weiss et al., 2013). Like their close chimpanzee cousins, captive gorillas show evidence for strong age-related declines in Extraversion (Kuhar et al., 2006), yet an Extraversion effect remained in gorillas.

Similarly, neither Conscientiousness nor Neuroticism appeared to be associated with longevity in chimpanzees. This difference between chimpanzees and

humans is probably attributable to the fact that associations between Conscientiousness and Neuroticism, and human mortality, may be attributable to the associations between these personality traits and health risk factors, e.g., because low Conscientiousness and high Neuroticism are related to cigarette smoking and alcohol consumption (Booth-Kewley & Vickers, 1994; Turiano et al., 2015). The present findings concerning chimpanzee Conscientiousness and Neuroticism support this account of Conscientiousness-mortality and Neuroticism-mortality associations in humans.

Although the other social dimensions of personality – Dominance and Extraversion – were not related to longevity, Agreeableness was, at very least in male chimpanzees. In other words, long-living captive male chimpanzees tend to be those who engage in positive social interactions characterized by cooperation, geniality, and being protective. The degree to which captive male chimpanzees are characterized by a preference for interacting with others, their competitive prowess and fearlessness, and, consequently, the ability to enjoy the spoils of rank, have no bearing on how long they live. This result can also be contrasted with the findings of Gilby et al. (2013) who found that male chimpanzees with the strongest degree of betweenness in their social network connections, i.e. males who tended to form coalitions with other males who themselves did not form many coalitions, derived the most fitness benefits. Though fitness and longevity have been linked and sociality appears to be relevant to both in male chimpanzees, the precise nature of the associations between fitness and longevity remains undetermined.

Female chimpanzees showed a different, unpredicted relationship between personality and longevity. High Openness female chimpanzees are those who were more curious, inventive, and inquisitive; these chimpanzees tended to live longer than low Openness counterparts. These findings are in line with meta-analytic results: a modest, positive effect of 'exploration' on survival, which was not significant in males or wild animals (Smith & Blumstein, 2008). Additionally, exploration did not have a significant effect on fitness in this meta-analysis.

Smith and Blumstein (2008) suggest that the effect of exploration is driven by directional selection, and these captive populations are becoming higher in Openness. Captive chimpanzees are protected from most acute environmental threats, e.g. predators. High Openness chimpanzees, who might be killed or mortally wounded while exploring wild environments, will no longer be selected out of the population in captivity. This is not the only possibility: Openness in both humans (Chamorro-Premuzic & Furnham, 2006) and chimpanzees (see chapter 2) is correlated with intelligence, which is well-known to be one of the most powerful predictors of survival in humans (Calvin et al., 2011). The effect of Openness in this sample may be tapping into the same underlying, much debated common sources of intelligence's correlation with longevity. However, despite its correlation with intelligence, Openness is not associated with longevity in humans, so without also studying intelligence, personality, and longevity together in chimpanzees, we are unable to derive further conclusions.

It is noteworthy that while longevity is a major life history variable, it does not directly represent the fitness of the animal. An individual may have higher fitness

because they live longer, simply due to having more time to produce offspring. The link might be subtler as well; longer living individuals may provide more for related offspring, improving personal fitness by increasing the fitness of others. However, there is no guarantee that longevity must lead to either of these effects in chimpanzees. A clear link between personality and these behaviors has yet to be established as well.

A trivial account could argue that all personality dimensions must affect fitness under some circumstance in some ways but not others, otherwise there would be no variation in personality. Many researchers focus on reproductive success as measure of fitness, and while this is arguably the most important life history trait, the presence of many differential psychological traits in chimpanzees suggests that each personality dimension came about due to different life history strategies (Nettle, 2006). In chimpanzees, our results suggest that Openness and Agreeableness were maintained in chimpanzees, at least partially, through their association with longevity.

Nevertheless, it remains an open question why Openness is specifically important for female longevity, and Agreeableness is only associated with male longevity. Ultimately, this study is a reminder of the complex, multifaceted nature of social relationships and rank; behavior and fitness in chimpanzees (de Waal, 2007). Moreover, whereas a large portion of research focuses on either males or females, working with a large sample of both sexes can give insight into common processes, or in our case, sex differences in how personality relates to longevity.

5 Comparing blood biomarkers of stress between chimpanzees and humans

5.1 Introduction

Like humans and other animals, both wild and captive primates experience stress, brought on by acute, challenging situations and problems (Edes, Wolfe, & Crews, 2016). These 'stressors', in addition to inducing behavioral changes, generate physiological responses (Cavigelli & Caruso, 2015).

The physiological response to stress is designed to promote survival of the organism (Edes et al., 2016), and it does this by activating the brain's neuroendocrine systems (Edes, 2017). When stressed, an animal's physiology is disrupted, and the stress response is designed to bring the organism's physiology back to non-stressful homeostasis (Nelson, 2005). This process is crucial to improving survival, and allowing individuals to continue to reproduce (McEwen & Lasley, 2002; Sterling, 2012). The physiological stress response inhibits both proceptive and receptive sexual behavior in both sexes (Sapolsky, Romero, & Munck, 2000), and upregulates the sympathetic nervous system, which while always active at a base level to maintain homeostasis, constricts blood flow necessary for fighting, fleeing, or sexual activity (Korte, Koolhaas, Wingfield, & McEwen, 2005).

Deviation from homeostasis thus occurs regularly, possibly many times a day (Edes & Crews, 2017). The normal variance that occurs in an animal's somatic systems is known as allostasis (Edes & Crews, 2017; McEwen & Stellar, 1993).

Allostasis reduces the costs of stressors, pushing the body toward recovery rather than exhaustion. This is an evolved adaptation for reducing the cost of stress, that also promotes reproduction, survival, well-being, and health, generally (Sterling, 2012). Nevertheless, repeated and/or prolonged exposure to stressors exacts a toll organisms, which is referred to as allostatic load (AL) (McEwen & Stellar, 1993). Exposure to even minor stressors accumulate, eventually damaging tissues, cells, and DNA (McEwen, 1998), and increasing an individual's risk of early mortality.

AL is not the property of a single system, but a process that develops throughout the entire body. As a result, assessing the amount of AL has been challenging, particularly as researchers must collect multiple physiological biomarkers and construct a composite from these data (Leahy & Crews, 2012). The most common biomarkers represent the states of the neuroendocrine, metabolic, and cardiovascular systems. The more biomarkers an individual has in dysregulation, i.e. observed to be outside the normal range for that marker, the higher their allostatic load.

The majority of AL research has been conducted in humans, in which AL has been linked to many mental and physical outcomes. Humans with higher allostatic load have poorer baseline physical performance, and are at greater risk for immunological disorder (McEwen, 1998), CVD (Seeman, Singer, Rowe, Horwitz, & McEwen, 1997), cognitive decline (Karlamangla et al., 2014), and early mortality (Gruenewald, Seeman, Ryff, Karlamangla, & Singer, 2006). As AL represents accumulation of negative effects over time, AL should increase with age, and biomarkers of AL match this hypothesis (Crimmins, Johnston, Hayward, & Seeman,

2003). Yet, demographic variables, including gender (Seeman, Singer, Ryff, Love, & Levy-Storms, 2002; Yang & Kozloski, 2011) and social or economic adversity (McEwen, 2012) are also related to allostatic load. Additionally, the extent of social support that one receives is associated with lower allostatic load (Seeman et al., 2002).

Animal researchers have studied allostatic load in nonhuman primates (see Edes and Crews (2017) for a review). An important early study estimated the costs of high and low social status in different species, and used this as a proxy for AL (Goymann & Wingfield, 2004). Goymann and Wingfield (2004) assessed five social characteristics of each species to determine the AL of relatively dominant and subordinate individuals. Rank acquisition and rank maintenance are costly to dominant individuals. Regularity and magnitude of threat from dominants and lack opportunities for subordinates to avoid dominant threats are costly to subordinates. The final criteria, food resource control and availability, can be costly to either dominants, subordinates, or both.

For example, in chimpanzees, it is costly to acquire and even costlier to maintain a dominant position in the social hierarchy, so dominant individuals were assigned high AL estimates. For subordinate chimpanzees, coping costs were estimated to be low and threats from dominants estimated to be modest, so subordinate chimpanzees were assigned lower AL (Mitani et al., 2002). In contrast, among savannah baboons, maintaining dominance is less costly, and threats from dominant individuals are more costly to subordinates, so dominant baboons had lower AL estimates relative to subordinate baboons (Sapolsky, 1982).

Goymann and Wingfield (2004), having estimated AL for individuals among many species, related AL to glucocorticoid concentration. In this study they examined six free-ranging, wild primate species - chimpanzees, mountain gorillas, long tailed macaques, savannah baboons, tufted capuchins, and ringtailed lemurs - and found that the ratio of dominant to subordinate AL estimates was positively associated with the ratio of glucocorticoid levels in dominant vs submissive individuals. So again, in chimpanzees, this indicated that dominant individuals, who were estimated to have higher AL than subordinate individuals, also had higher glucocorticoid levels.

Maestripieri and Hoffman (2011) later found impacts from many AL markers, including glucocorticoids, cytokines, proteins, and cholesterols, on the health and reproductive fitness of free-ranging rhesus macaques. Most recently, Edes and colleagues (2016) examined allostatic load markers in captive gorillas. These researchers gathered a comprehensive set of biomarkers, including albumin, cholesterol, cortisol, creatinine, glucose, and triglycerides, and performed a principle components analysis of the markers. The second component, which was composed of albumin, glucose and interleukin-6, was lower in females, higher in older gorillas, and associated with high triglyceride levels and earlier mortality (Edes et al., 2016).

A few studies have examined AL biomarkers in chimpanzees, yet most have measured only cortisol (Anestis, 2005; Anestis, Bribiescas, & Hasselschwert, 2006; Goymann & Wingfield, 2004; Muller & Wrangham, 2004; Whitten, Stavisky, Aureli, & Russell, 1998). Lambeth, Hau, Perlman, Martino, and Schapiro (2006) were notable for examining the effects of positive reinforcement training on glucose,

haematocrit, neutrophil, and white blood cell levels. Among chimpanzees exposed to a stressful procedure (injection), those who were trained and familiar with the procedure also showed lower glucose, neutrophil, and white blood cells levels than untrained individuals. Also in chimpanzees, high levels of non-physiological AL biomarkers such as body mass index (BMI) (Videan, Fritz, & Murphy, 2007) and blood pressure (Ely, Zavaskis, & Lammey, 2013) have also been linked to the ageing process in chimpanzees.

Videan et al. (2009) sampled biomarkers related to oxidative stress and cardiovascular risk, and produced the most comprehensive report on chimpanzee biomarkers to date. By comparing ten male chimpanzees with ten male humans, they found that the chimpanzees had significantly higher levels of insulin, insulin-like growth factor, fibrinogen, lipoprotein, and white blood cells, all cardiovascular risk factors in humans. These differences were attributed to chimpanzees' high risk for cardiovascular disease, and especially cardiomyopathy, which is the leading cause of death in chimpanzees (Chilton, Wilcox, Lammey, & Meyer, 2016; Lammey, Lee, Ely, & Sleeper, 2008; Laurence et al., 2017). However, although heart conditions are also common in humans, the major cause of heart disease differs between these two species. Humans tend to develop heart conditions as a result of atherosclerosis, or clogged arteries, whereas chimpanzees are much more likely to suffer from myocardial fibrosis, a thickening and stiffening of heart tissue, which can cause death through cardiac arrhythmia (Varki et al., 2009).

Although Videan et al.'s (2009) study compared chimpanzees and humans, their small sample size, which included only males, limited the generalizability of

their findings. We thus sought to examine a much larger sample of both male and female chimpanzees. Additionally, as most prior studies of stress and AL in primates have only looked at a few targeted physiological markers, we decided to take a bottom-up approach. We did not select biomarkers based on findings from prior research, but drew our measures from a complement of physical and blood tests which were available in humans and in chimpanzees. We wished to examine the entire system of biomarkers, since many of these markers and their relationships with one another have not yet been explored in chimpanzees.

The present study's aims were thus to examine the emergent structure of AL, as determined from an opportunistic sample of physical health characteristics and blood biomarkers, and to test whether structure and correlates of AL are similar in chimpanzees and humans. We advance three predictions. First, given what we know about AL in gorillas and humans (Edes et al., 2016), we would expect to find that the same biomarkers relate to allostatic load in chimpanzees. Second, we expect AL to be higher in older chimpanzees. Third, sex also relates to AL in both humans and gorillas (Edes & Crews, 2017), though males and females appear to have different weakness when it comes to different biomarkers (Juster, McEwen, & Lupien, 2010). We predict that in chimpanzees, sex will also have an effect on AL biomarkers.

5.2 Methods

5.2.1 Subjects

5.2.1.1 Chimpanzees

Physiological data were collected between 1996 and 2004 from 177 chimpanzees living at the Yerkes National Primate Research Centre (YNPRC). Both

blood chemistry and haematological panels were obtained. Up to four samples were taken over the course of the study period. Physical measurements, including BMI and blood pressure were measured up to three times between 2005 and 2011. Chimpanzees' ages during the study period ranged from 3 to 48 years.

5.2.1.2 Humans

Human participants were drawn from the National Health and Nutrition Examination Survey (NHANES), a study of men and women living in the USA. Participants' ages ranged between 1 and 90 years. 29,314 individuals were involved in the biomarker collection wave, during which a variety of blood serum panels were collected from participants; blood pressure and BMI were also measured.

5.2.2 Biomarkers

Test results from standard complete blood, comprehensive metabolic, lipid profile, and liver panels were available in both samples. We also used body mass index (BMI), and diastolic and systolic blood pressures measurements from both samples. A summary of overlapping biomarkers is shown in Table 5.1. Variables were scaled and centered prior to analyses, all biomarkers except for BMI were scaled across the entire human and chimpanzee sample. BMI was scaled independently for humans and chimpanzees.

5.2.3 Analyses

To explore the structure of our biomarker data, we used principal components analysis (PCA) and exploratory factor analysis (EFA). To confirm our exploratory findings, we used confirmatory factor analysis (CFA), and compared structure between groups with measurement invariance testing.

Measurement invariance tests the extent to which model structure, in our case CFA model structure, is invariant across groups. In other words, measurement invariance tests whether the best fitting model constrains loadings (slopes), intercepts, residuals, and other parameters to be the same across groups. The level of invariance is determined by the type of parameter which is fixed between the groups; with 'strong' invariance, loadings and intercepts are both fixed, and one can directly compare path coefficients between groups (Sass, 2011).

Standard measurement invariance testing assesses all parameters of a certain type at once, e.g., a model wherein all intercepts were fixed across groups would be compared to an identical model except that all these intercepts would be allowed to be estimated within rather than across groups. Partial measurement invariance provides a framework for testing invariance of individual parameters (Millsap, Olivera-Aguilar, & Hoyle, 2012); to extend the last example, partial measurement invariance testing of intercepts would indicate which individual intercept would improve model fit the most by being freed, i.e. estimated separately within groups. Using a step-wise 'tear-down' strategy, starting with all parameters of interest included and testing if freeing individual parameters improve fit, partial invariance identifies weak parameters. Subsequent rounds of partial invariance testing allow one to determine which parameters are invariant across groups.

Table 5.1

Descriptive statistics for both chimpanzee and human biomarker samples

	Chimpanzees			Humans		
Biomarker	N	M	SD	N	M	SD
WBC	171	12.08	4.30	26372	7.39	2.35
RBC	171	5.18	0.45	26370	4.63	0.46
HCT	171	42.25	3.70	26370	40.16	4.24
HGB	171	13.95	1.50	26372	13.48	1.52
MCV	171	81.60	4.16	26371	86.99	6.30
MCH	171	26.87	1.58	26369	29.20	2.41
MCHC	171	32.99	0.79	26369	33.55	0.91
Lymphocytes	171	39.23	17.77	8150	37.30	13.50
Monocytes	171	2.39	1.41	8150	5.59	3.10
Eosinophils	171	2.01	1.46	8150	2.95	3.23
Glucose	171	101.27	14.99	18719	99.10	36.21
BUN	171	12.72	6.68	18723	14.06	5.86
Creatinine	171	1.09	0.45	18723	1.07	0.37
Protein	171	7.65	1.39	18723	7.41	0.47
Albumin	171	3.59	0.36	18723	4.16	0.39
Bilirubin	171	0.23	0.11	18723	0.59	0.34
ALP	171	171.10	156.95	18721	100.99	64.81
SGPT	171	32.94	11.64	18723	17.24	16.00
SGOT	171	26.30	14.48	18723	22.10	14.88
Cholesterol	171	198.92	38.96	23561	193.23	44.77
Calcium	171	9.91	2.54	18722	9.31	0.44
Phosphates	171	3.03	1.07	18723	3.56	0.58
Sodium	171	140.20	4.28	18723	141.27	2.48
Potassium	171	3.80	2.23	18723	4.06	0.33
Chloride	171	100.80	4.06	18723	104.46	3.34
Globulins	171	3.96	0.65	14056	3.30	0.47
Triglycerides	171	108.32	42.39	23515	130.25	103.42
GGTP	171	30.77	28.84	14549	31.53	49.39
Osmolality	171	278.38	5.46	14056	279.56	6.52
BMI	60	95.07	15.16	27830	23.80	6.78
Systolic BP	91	136.23	20.95	23756	118.58	21.15
Diastolic BP	91	74.01	15.98	23044	68.95	14.27

Note. WBC = white blood cells, RBC = red blood cells, HCT = hematocrit, HGB = hemoglobin, MCV = mean corpuscular volume, MCH = mean corpuscular hemoglobin, MCHC = mean corpuscular hemoglobin concentration, BUN = blood urea nitrogen, ALP = alkaline phosphatase, SGPT = serum glutamate-pyruvate transaminase, SGOT = serum glutamic axaloacetic transaminase, GGTP = gamma-glutamyltransferase, BMI = body mass index, BP = blood pressure

5.3 Results

Because our samples did not contain cortisol, interleukin-6, and other common AL biomarkers, we wished to establish which biomarkers, out of those available, might effectively measure AL in this sample. We also wanted to duly consider the markers that would be most likely to be associated with AL, based on earlier work in primates (Edes & Crews, 2017).

We therefore randomly divided the NHANES sample into exploratory and confirmatory subsamples of 9000 participants each. Our exploratory analyses were exclusively based on the first subsample. Our confirmatory analyses were confined to the second human subsample and to the chimpanzee sample.

5.3.1 Suitability of data

To check whether the data were suitably factorable, we applied Bartlett's test of sphericity to the correlation matrices of the both the exploratory human sample and chimpanzee sample. The chimpanzee data ($\chi^2 = 1740$, $p < 0.001$, $df = 496$) and the human data ($\chi^2 = 147700$, $p < 0.001$, $df = 496$) contained sufficient correlations for us to proceed with further analyses.

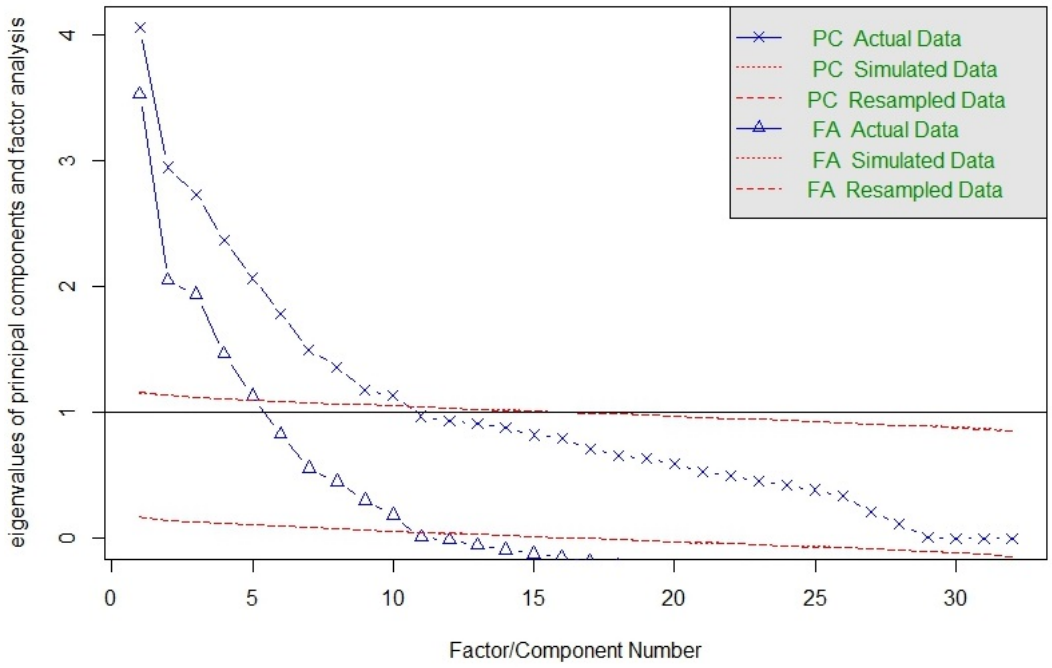
5.3.2 Exploratory Analyses

We used the 'fa.parallel' and 'nfactors' function of the R 'psych' package (Revelle, 2015) to investigate the number of factors (Figure 5.1). Parallel analysis suggested 10 components (and factors); Ruscio & Roche's Comparison Data suggested 9; Velicer's Map Criterion reached a local minimum at 5; Very Simple Structure reached a local maximum at 7, and the scree plot did not indicate any obvious cut-off. In general, the methods used to determine the number of

components/factors we ought to extract were either inconsistent or similarly unclear in their results.

Figure 5.1

Parallel analysis scree plots



Note. PC = Principal Component, FA = Factor (Analysis).

Therefore, we chose to extract multiple structures of between 5 and 10 factors/components to explore the clustering of AL biomarkers. We used PCA for our initial data reduction; Table 5.2 shows the loadings of variables on the clearest AL component from each extraction. All variables with a loading higher than ≥ |0.3| on an AL component in any of the extractions are shown.

Table 5.2

Loadings of biomarkers on a theoretical AL component

	Components in solution					
Biomarkers	5	6	7	8	9	10
Systolic BP	**0.71**	**0.61**	**0.67**	**0.69**	**0.50**	**0.61**
Diastolic BP	**0.67**	**0.67**	**0.74**	**0.75**	0.45	0.45
BMI	**0.69**	**0.70**	**0.72**	**0.71**	**0.72**	**0.48**
Cholesterol	**0.59**	**0.46**	**0.50**	**0.52**	**0.37**	**0.70**
Triglycerides	**0.50**	**0.37**	0.32	0.34	0.29	**0.65**
Glucose	**0.42**	0.27	0.17	0.22	0.29	**0.61**
Albumin	-0.32	-0.39	-0.29	-0.30	**-0.60**	-0.21
Lymphocytes	-0.33	-0.31	-0.24	-0.24	**-0.43**	0.03
Globulins	0.22	0.03	-0.27	0.30	**0.43**	0.10
Bilirubin	-0.07	-0.06	-0.15	-0.14	**-0.36**	-0.11
Phosphates	**-0.41**	**-0.57**	**-0.51**	**-0.51**	-0.14	-0.12
ALP	**-0.27**	**-0.40**	**-0.44**	**-0.43**	0.00	0.06
Calcium	-0.16	-0.38	-0.21	-0.21	-0.29	0.07
Hematocrit	0.35	0.32	0.29	0.29	0.14	0.13
Hemoglobin	0.33	0.29	0.27	0.25	0.11	0.14
BUN	0.30	0.09	0.07	0.12	-0.02	0.22
Creatinine	0.30	0.10	0.09	0.16	-0.05	0.09

Note. BP = blood pressure, BMI = body mass index, ALP = alkaline phosphatase, BUN = blood urea nitrogen. Bolding indicates that this was the highest loading for that variable.

EFA is frequently used for allostatic load models, but latent variables, which are the 'factors' used in EFA, are theoretically questionable for modelling AL (Crook & Booth, 2017). Because we wished to use latent variables in a CFA framework for subsequent analyses, we performed EFAs of the solutions with the most components (10; Table 5.3) and fewest components (5; Table 5.4), and compared the factor solutions to PCAs with the same number of components. All component and factor loadings were nearly identical, so we proceeded with a confirmatory factor analysis.

Table 5.3

PCA solution for 10 extracted components of human biomarkers

Loadings	1	2	3	4	5	6	7	8	9	10
RBC	**0.90**	-0.36	0.07	0.07	-0.02	-0.00	0.02	0.08	0.00	0.00
HCT	**0.90**	0.30	0.13	0.08	0.03	0.04	-0.07	0.05	0.01	0.06
HGB	**0.87**	**0.41**	0.14	0.10	0.02	0.02	-0.04	0.07	-0.03	0.02
MCV	0.05	**0.91**	0.10	0.03	0.07	0.06	-0.14	-0.07	0.00	0.09
MCH	0.08	**0.97**	0.11	0.06	0.04	0.03	-0.09	-0.02	-0.06	0.04
MCHC	0.10	**0.56**	0.06	0.08	-0.04	-0.06	0.10	0.09	-0.18	-0.14
Glucose	0.02	-0.10	**0.61**	0.07	0.17	-0.15	0.16	-0.07	-0.13	0.10
Cholesterol	0.00	0.17	**0.70**	-0.03	0.03	-0.02	-0.12	0.05	0.09	-0.08
Triglycerides	0.06	0.06	**0.65**	0.17	0.04	-0.08	0.05	-0.00	-0.11	-0.25
Systolic BP	0.12	0.14	**0.61**	0.01	0.21	0.06	-0.32	-0.12	0.19	0.06
BMI	0.24	0.13	**0.48**	0.02	-0.12	0.09	-0.23	**-0.45**	0.22	-0.04
SGPT	0.18	0.02	0.03	**0.83**	-0.03	0.03	-0.03	0.01	0.04	-0.07
SGOT	0.03	0.07	-0.03	**0.89**	0.02	-0.02	0.01	0.04	0.11	0.02
GGTP	-0.02	0.04	0.18	**0.74**	-0.01	-0.01	0.06	-0.05	0.06	0.09
BUN	-0.07	0.04	0.22	-0.03	**0.82**	0.08	-0.05	0.04	-0.08	-0.03
Creatinine	0.04	0.01	0.09	0.03	**0.81**	-0.04	-0.17	0.04	0.02	0.01
Potassium	0.06	0.07	-0.09	-0.03	**0.43**	0.13	0.28	-0.12	0.13	0.15
Sodium	0.11	0.04	-0.05	0.00	0.13	0.89	0.02	0.13	0.01	-0.01
Chloride	-0.12	0.02	-0.21	-0.02	-0.10	**0.72**	-0.08	-0.08	-0.15	-0.06
Osmolality	0.09	-0.12	0.28	0.05	**0.47**	**0.60**	0.14	-0.07	-0.02	0.08
ALP	0.07	-0.08	0.06	0.13	-0.07	-0.01	**0.73**	0.01	0.00	0.14
Phosphates	0.06	0.07	-0.09	-0.03	**0.43**	0.13	0.28	-0.12	0.13	0.15

Diastolic BP	0.27	0.13	**0.45**	0.10	0.02	0.09	**-0.50**	-0.11	0.22	0.06
Lymphocytes	-0.26	-0.34	0.03	0.17	-0.17	0.07	-0.04	**0.56**	-0.03	0.19
Albumin	0.39	0.14	-0.21	-0.07	0.00	0.01	0.04	**0.72**	0.02	-0.08
Calcium	0.22	0.10	0.07	-0.09	0.06	0.04	0.31	**0.58**	0.28	-0.13
Protein	0.16	-0.08	-0.06	0.12	0.03	-0.11	0.07	0.39	**0.82**	-0.03
Globulins	-0.16	-0.21	0.10	0.19	0.01	-0.11	0.04	-0.18	**0.82**	0.03
WBC	0.1	-0.05	0.01	-0.02	0.08	-0.14	0.18	-0.26	0.05	**-0.74**
Monocytes	0.12	0.01	-0.10	0.04	0.13	-0.15	0.00	-0.17	0.08	**0.56**
Eosinophils	0.03	-0.05	-0.02	0.00	0.02	-0.01	0.24	-0.04	-0.05	**0.46**
Bilirubin	0.28	0.09	-0.11	0.24	0.16	-0.15	-0.11	0.26	-0.27	0.05

Note. Variables sorted by primary loading. Loadings are bolded for all values ≥ |0.4|.

Table 5.4

PCA solution for 5 extracted components of human biomarkers

Loadings	1	2	3	4	5
Cholesterol	**0.59**	0.00	0.04	0.05	0.07
BMI	**0.69**	-0.02	0.08	0.05	-0.04
Systolic BP	**0.71**	0.01	0.05	0.07	0.21
Diastolic BP	**0.67**	0.12	0.12	0.12	0.06
Triglycerides	**0.50**	0.03	0.01	0.17	0.05
Phosphates	**-0.41**	0.10	-0.15	0.07	0.06
Glucose	**0.42**	-0.02	-0.16	0.12	0.15
Lymphocytes	-0.33	-0.01	-0.29	0.20	0.01
ALP	-0.27	0.16	-0.18	0.24	0.05
RBC	0.19	**0.81**	-0.21	0.00	0.01
HCT	0.35	**0.78**	0.38	0.07	0.04
HGB	0.33	**0.76**	0.48	0.09	0.02
Albumin	-0.32	**0.69**	0.15	-0.05	0.01
Calcium	-0.16	**0.54**	-0.08	0.04	0.12
Protein	-0.02	**0.45**	-0.39	0.32	-0.09
MCH	0.25	-0.01	**0.82**	0.10	0.05
MCV	0.22	0.03	**0.88**	0.11	0.02
MCHC	0.03	0.12	**0.54**	0.08	-0.08
Globulins	0.22	-0.10	**-0.54**	0.38	-0.11
SGOT	-0.02	0.03	0.08	**0.87**	-0.03
SGPT	0.06	0.14	0.09	**0.77**	-0.03
GGTP	0.11	-0.06	0.03	**0.74**	0.01
Osmolality	0.15	0.03	-0.07	0.08	**0.80**
Sodium	-0.19	0.12	0.17	-0.01	**0.68**
BUN	0.30	-0.06	-0.01	-0.03	**0.67**
Creatinine	0.30	0.05	-0.04	0.02	**0.55**
Potassium	-0.06	0.06	-0.03	0.04	**0.41**
Chloride	-0.28	-0.20	0.21	-0.09	0.36
Eosinophils	-0.14	0.02	-0.05	0.08	0.09
Bilirubin	-0.07	0.30	0.22	0.15	0.02
Monocytes	0.03	0.03	-0.00	0.11	0.04
WBC	0.17	0.04	-0.12	-0.10	-0.12

Note. Variables sorted by primary loading. Loadings are bolded for all values ≥ |0.4|.

5.3.3 Confirmatory Analyses

We modelled the 10 and 5 factor solutions to obtain model fits with our confirmatory dataset, using three common measures: Comparative Fit Index (CFI), an incremental fit index based on model non-centrality; Root Mean Square Error of Approximation (RMSEA), an absolute index based on non-centrality; Standardized Root Mean Residual (SRMR), an absolute index with no penalty for model complexity (Hu & Bentler, 1999). Model fits for these solutions were poor (Table 5.5), and the 10 factor model was unable to compute standard errors for the chimpanzee data.

Table 5.5

CFA model fit statistics for models containing all variables

CFA model	χ^2	df	CFI	RMSEA	SRMR.
10 factors		433			
Human	155709		0.417	0.201	0.137
Chimpanzee	1394		0.482	0.201	0.174
5 factors		274			
Human	152344		0.417	0.250	0.144
Chimpanzee	1230		0.550	0.140	0.157

Note. df = degrees of freedom, CFI = Comparative Fit Index, RMSEA = Root Mean Squared Error of Approximation, SRMR = Standardized Root Mean square Residual

The poor fit of these models indicated that interpreting the entire system of biomarkers in CFA would be problematic in both chimpanzees and humans, despite our sizable samples. Thus, we constrained our models to the biomarkers associated with AL, and examined CFAs with a single AL factor.

We fit our first model with the broadest set of biomarkers which had at least 4 primary loadings across our exploratory factor analyses. This model included cholesterol, triglycerides, phosphates, alkaline phosphatase, BMI, and systolic and diastolic blood pressure (Table 5.2). According to the absolute fit indices RMSEA, and SRMR, the fit of this model was considerably better than our models of all biomarkers (compare Tables 5.5 and 5.6).

We sought to improve the model further by eliminating biomarkers which less frequently loaded with the other relevant markers, and looking for improvements in model fit (Table 5.6). First, we removed alkaline phosphatase, which improved CFI, RMSEA, and SRMR in models of the chimpanzee sample, and improved CFI and SRMR in the human sample. The RMSEA of the human models increased by a small amount (0.02), but otherwise, removing alkaline phosphatase improved model fit. Second, we removed phosphates, which did not obviously improve model fit, so we returned phosphates to the model. As the CFI of our phosphates-inclusive model was greater than 0.9, we chose to proceed with measurement invariance testing (Millsap et al., 2012) to compare model fit among the two species groups.

Table 5.6

Fit statistics for single AL CFA models

Model containing	$\chi 2$	df	CFI	RMSEA	SRMR
D, S, T, C, P, BMI, ALP		20			
Human	1797		0.833	0.101	0.066
Chimpanzee	60.97		0.763	0.108	0.108
D, S, T, C, P, BMI		9			
Human	831.3		0.911	0.103	0.050
Chimpanzee	14.02		0.958	0.056	0.066
Both (jointly estimated)	846.6		0.910	0.103	0.051
D, S, T, C, BMI		14			
Human	897.2		0.907	0.085	0.049
Chimpanzee	26.88		0.898	0.072	0.085

Note. df = Degrees of Freedom, CFI = Comparative Fit Index, RMSEA = Root Mean Squared Error of Approximation, SRMR = Standardized Root Mean Residual, D = Diastolic blood pressure, S = Systolic blood pressure, T = Triglycerides, C = Cholesterol, P = Phosphates, BMI = Body Mass Index, ALP = Alkaline Phosphatase.

We first tested for the degree of measurement invariance between the NHANES and YNPRC samples. Across all six variables, the model with factor loadings estimated across both groups was a significantly poorer fit than the base model, wherein all parameters were freely estimated within the two groups (χ^2 = 54.9, df = 5, $p < 0.001$), indicating that measurement invariance would not hold for all these variables at once.

We thus proceeded with partial measurement invariance testing, beginning with tests of metric invariance, where we tested if the loadings of each variable on the AL factor were the same across groups (Table 5.7). The highest χ^2 value was for diastolic BP, so we freed its loading on the AL variable. On the second pass, systolic BP emerged with the highest χ^2, so we freed it as well. In the next iteration, no χ^2 values were significant, so we left the remaining parameters fixed.

Table 5.7

Metric partial invariance tests of single AL CFA model

	Model 1		Model 2		Model 3	
Fixed parameters	χ^2	p	χ^2	p	χ^2	p
Cholesterol	0.77	0.38	3.22	0.12	0.15	0.70
Triglycerides	17.05	0.002	19.23	< 0.001	0.38	0.70
Systolic BP	3.29	0.13	31.71	< 0.001		
Diastolic BP	17.56	0.002				
BMI	2.65	0.13	1.89	0.21	0.53	0.70
Phosphates	2.57	0.13	1.52	0.22	4.93	0.11

Note. BP = Blood pressure, all degrees of freedom were equal to 1. All p-values were adjusted for multiple comparisons using Benjamini and Hochberg's False Discovery Rate. Bolding indicates parameters which were found to be invariant.

We followed the same approach to assess our model's partial scalar invariance, where we individually tested if the intercepts on each observed variable could be fixed across groups (Table 5.8). Testing scalar invariance was not strictly necessary to be able to compare association patterns between groups, but is nevertheless informative of the presence of measurement bias or developmental differences (Byrne & Watkins, 2003). We freed systolic BP, then phosphates, and finally triglycerides. The remaining parameters were fixed. We also attempted to establish strict partial invariance, that is, invariance in the residuals of our observed variables, but were unable to establish that residuals were invariant between these two groups.

With these particulars of invariance established, we fit a model that included partial invariance in intercepts and loadings, as indicated. We compared the fit of this model to a model in which all parameters were jointly estimated across the groups and a model in which parameters were freely estimated within groups (Table 5.9).

Overall, the CFI and SRMR indicated that all the models had good fits (Hu &

Bentler, 1999), but neither CFI nor SRMR pointed to any model having clearly better fit than another. However, the RMSEAs of both models which do not take into account partial invariance, were above the 'unacceptable' threshold of 0.1 (Chen, Curran, Bollen, Kirby, & Paxton, 2008). As such, we concluded that the model which includes partially invariant fixed parameters was the best of the three. This final model is presented in Table 5.10.

Table 5.8

Scalar partial invariance tests of single AL CFA model

	Model 1		Model 2		Model 3		Model 4	
Fixed parameters	$\chi 2$	p	$\chi 2$	p	$\chi 2$	p	$\chi 2$	p
Cholesterol	0.19	0.66	2.14	0.18	2.79	0.13	0.02	0.89
Triglycerides	32.90	< 0.001	12.06	0.001	8.30	0.009		
Systolic BP	44.49	< 0.001						
Diastolic BP	2.60	0.13	6.95	0.14	8.07	0.009	2.07	0.23
BMI	3.19	0.11	1.56	0.21	1.29	0.26	4.23	0.12
Phosphates	34.57	< 0.001	36.79	< 0.001				

Note. BP = Blood pressure, all degrees of freedom were equal to 1. All p-values were adjusted for multiple corrections using Benjamini and Hochberg's False Discovery Rate. Bolding indicates parameters which were found to be invariant.

Table 5.9

Fit statistics for different group models

Model	$\chi 2$	df	CFI	RMSEA	SRMR
Partial invariances included	873.9	25	0.909	0.088	0.55
Joint estimation across groups	846.6	9	0.910	0.103	0.51
Free estimation between groups	845.5	18	0.912	0.102	0.50

Note. df = Degrees of Freedom, CFI = Comparative Fit Index, RMSEA = Root Mean Squared Error of Approximation, SRMR = Standardized Root Mean Residual.

Table 5.10

Parameters of best fit partially invariant AL CFA model

	Estimate	SE	z	p
Humans				
Loadings on AL				
Cholesterol †	0.520	0.012	41.834	< 0.001
Triglycerides †	0.359	0.013	27.733	< 0.001
Systolic BP	0.800	0.011	71.436	< 0.001
Diastolic BP	0.799	0.012	68.948	< 0.001
BMI †	0.609	0.011	53.865	< 0.001
Phosphates †	-0.314	0.017	-18.261	< 0.001
Intercepts				
Cholesterol †	-0.045	0.012	-3.856	< 0.001
Triglycerides	-0.030	0.012	-2.579	0.01
Systolic BP	-0.080	0.012	-6.896	< 0.001
Diastolic BP †	-0.106	0.012	-8.969	< 0.001
BMI †	0	0.011	0	1
Phosphates	0.107	0.014	7.410	< 0.001
AL	0			
Variances				
Cholesterol	0.735	0.014	54.285	< 0.001
Triglycerides	0.876	0.015	57.870	< 0.001
Systolic BP	0.376	0.011	35.667	< 0.001
Diastolic BP	0.388	0.011	35.705	< 0.001
BMI	0.626	0.012	52.559	< 0.001
Phosphates	0.924	0.018	52.268	< 0.001
AL	1			
Chimpanzees				
Loadings on AL				
Cholesterol †	0.520	0.012	41.834	< 0.001

Triglycerides †	0.359	0.013	27.733	< 0.001
Systolic BP	0.958	0.109	8.782	< 0.001
Diastolic BP	1.156	0.114	10.181	< 0.001
BMI †	0.609	0.011	53.865	< 0.001
Phosphates †	-0.314	0.017	-18.261	< 0.001
Intercepts				
Cholesterol †	-0.045	0.012	-3.856	< 0.001
Triglycerides	-0.048	0.073	-0.716	0.51
Systolic BP	-0.088	0.063	-1.402	0.16
Diastolic BP †	-0.106	0.012	-8.969	< 0.001
BMI †	0	0.011	0	1
Phosphates	0.042	0.077	0.545	0.59
AL	0.139	0.940	1.478	0.14
Variances				
Cholesterol	0.931	0.114	8.175	< 0.001
Triglycerides	0.842	0.097	8.653	< 0.001
Systolic BP	0.323	0.088	3.653	< 0.001
Diastolic BP	0.019	0.115	0.166	0.868
BMI	1.144	0.221	5.176	< 0.001
Phosphates	0.966	0.110	8.805	< 0.001
AL	1			

Note. BP = blood pressure, BMI = body mass index, AL - allostatic load, † Fixed parameters, jointly estimated across groups.

5.3.4 Associations of biomarkers with age and sex

Age and sex have been repeatedly shown to be important variables relating to AL (Juster et al., 2010). Age, sex, and AL biomarkers have even been studied in concert, in this NHANES sample (Yang & Kozloski, 2011). We examined a third variable, species, in conjunction with age and sex (Table 5.11). To account for chimpanzees' shorter lifespans compared to humans, we scaled chimpanzee ages by 1.5 (Napier & Napier, 1967) to put them on approximately the same scale as humans. As expected, except for BMI in chimpanzees, age was associated with higher AL. Sex was associated with all AL markers in humans, but appeared not to have any significant effects in the chimpanzee sample.

Table 5.11

Statistics associating age and AL biomarkers within species

	Age - *r*		Sex - *d*	
Biomarker	Humans	Chimpanzees	Humans	Chimpanzees
Cholesterol	0.50 **	0.30 **	-0.11 **	0.05
Triglycerides	0.24 **	0.31 **	0.08 **	0.13
Systolic BP	0.71 **	0.25 *	0.17 **	0.24
Diastolic BP	0.50 **	0.47 **	0.21 **	0.10
BMI	0.52 **	-0.09	-0.16 **	0.09
Phosphates	-0.30 **	-0.32 **	-0.18 **	0.16

Note. BP = Blood pressure, *r* = Pearson's product-moment correlation coefficient, *d* = Cohen's measure of effect size. For sex, males were coded as 1, and females as 2; a positive d would indicate that the mean of males was larger than females, and vice versa.
* p = 0.02, ** p < 0.001

To test for potential interactions, we ran a three-way multivariate analysis of covariance (MANCOVA) on the same six AL biomarkers, with sex, species, age, and their interactions as predictors (Table 5.12).

Table 5.12

Results of MANCOVA on AL biomarkers, age, sex, and species

Outcome	η^2	*B*	*F*	p
Multivariate				
Age	0.491		890.37	< 0.001
Species	0.045		42.73	< 0.001
Sex	0.076		76.64	< 0.001
Age x Species	0.011		9.49	< 0.001
Age x Sex	0.048		48.29	< 0.001
Species x Sex	0.001		1.27	0.27
Age x Species x Sex	0.002		2.26	0.035
Cholesterol				
Age		0.42	1334.58	< 0.001
Species		0.13	0.26	0.61
Sex		0.01	16.82	< 0.001
Age x Species		0.05	0.12	0.73
Age x Sex		0.21	52.48	< 0.001
Species x Sex		-0.12	0.14	0.71
Age x Species x Sex		-0.22	0.29	0.59
Triglycerides				

Age	0.23	287.93	< 0.001
Species	-0.30	2.58	0.11
Sex	-0.17	19.94	< 0.001
Age x Species	0.02	0.18	0.67
Age x Sex	0.10	7.95	0.005
Species x Sex	0.12	0.24	0.62
Age x Species x Sex	-0.20	0.19	0.66
Systolic Blood Pressure			
Age	0.58	3678.29	< 0.001
Species	0.92	88.30	< 0.001
Sex	-0.33	145.72	< 0.001
Age x Species	0.43	1.25	0.26
Age x Sex	0.23	96.97	< 0.001
Species x Sex	0.00	0.32	0.57
Age x Species x Sex	-0.98	9.80	0.002
Diastolic Blood Pressure			
Age	0.30	606.48	< 0.001
Species	0.08	0.10	0.76
Sex	-0.28	193.29	< 0.001
Age x Species	1.20	13.46	< 0.001
Age x Sex	-0.01	0.41	0.53
Species x Sex	0.07	0.65	0.42
Age x Species x Sex	-0.95	7.96	0.005
BMI			
Age	0.17	196.77	< 0.001
Species	-0.20	7.26	0.007
Sex	0.12	32.89	< 0.001
Age x Species	-0.56	7.46	0.006
Age x Sex	0.04	2.40	0.12
Species x Sex	-0.29	1.57	0.21
Age x Species x Sex	0.11	0.08	0.77
Phosphates			
Age	-0.48	487.45	< 0.001
Species	-1.05	102.24	< 0.001
Sex	0.04	55.19	< 0.001
Age x Species	-0.97	23.25	< 0.001
Age x Sex	0.32	127.58	< 0.001
Species x Sex	-0.45	3.37	0.067
Age x Species x Sex	0.05	0.01	0.91

Note. All degrees of freedom were equal to 1. For binary variables sex and species, females and chimpanzees were assigned 1, respective to their categories. The estimated *F* value for the multivariate outcome is approximate, generated from the Pillai-Bartlett statistic. $\eta 2$ = partial eta-squared effect size.

For the multivariate AL outcome, we found unambiguously significant differences for age, species, sex, and the interactions of age with species and sex. At the univariate level, age and sex were associated with every biomarker; older individuals had higher AL, and females had lower AL, which agrees with the correlational results in Table 5.11. We found a significant effect of species for some biomarkers, but the directions of the relationships were not consistent. Similarly, some species x age effects were significant, and a significant difference was found overall, but again, the direction of effects was inconsistent. Age x sex effects were significant overall, and reliably indicated that females tend to have more of each biomarker measure as they age, regardless of species. However, except for age, effect sizes were generally medium (< 0.13) to small (< 0.02) (Miles & Shevlin, 2001).

5.4 Discussion

When examining the component and factor structures of human and chimpanzee blood, cardiovascular, hepatorenal, and metabolic biomarkers, we found evidence that allostatic load could be modelled from multisystem markers in both species. We were unable to find models with adequate fit that incorporated our entire panel of biomarkers. However, by incorporating only biomarkers which we believed might be relevant to AL, we constructed a model with good fit for both chimpanzees and humans. In these two samples, our results suggest that systolic and diastolic blood pressure, cholesterol, triglycerides, and BMI are positively associated with higher AL, and that phosphates are negatively associated with AL, in both humans and chimpanzees.

With the exception of phosphates, all of these markers have been used to calculate allostatic load in humans and in nonhuman primates (Edes & Crews, 2017). Indeed, our selection of models and latent variables (Table 5.2) relied a on pre-existing understanding of AL biomarkers in chimpanzees (Lambeth et al., 2006; Videan et al., 2009) and other primate species (Edes & Crews, 2017). Phosphates are not well- represented in the AL literature, but allostasis in phosphate regulation has been noted in the cardiovascular and renal systems of aging mammals (Ohnishi & Razzaque, 2010), and so the relevance of phosphates in our models is not surprising.

Some biomarkers did not appear to contribute to AL in our PCAs with the human sample. Glucose is commonly used in AL models because of its connection to diabetes and metabolic processes (Stumvoll, Tataranni, Stefan, Vozarova, & Bogardus, 2003), but while it twice assumed a primary loading with other AL biomarkers (Table 5.2), in the majority of our PCAs it did not. Creatinine is another common AL marker (Juster et al., 2010), and it also did not assume a primary loading with the other AL variables. Instead, creatinine tended to cluster with blood urea nitrogen, potassium, and osmolality (Tables 5.3, 5.4). These markers are associated with dietary sodium intake and subsequent renal health issues (Berge-Landry & James, 2004). However, Berge-Landry and James (2004) did not find that cholesterol or triglycerides were associated with dietary differences in sodium consumption, so it may be that creatinine captures particular renal or hepatorenal allostasis, but not cardiovascular allostasis.

The structure of the associations between AL and these biomarkers differed slightly between chimpanzees and humans. Both systolic and diastolic blood pressure

loaded more strongly on the latent AL variable in chimpanzees than in humans, but otherwise the loadings were invariant across species. The blood pressure differences may be the result of the anatomical differences between humans and chimpanzees, such as changes in muscular and vascular tissues, which were necessary to support humans' upright locomotion (Diogo, Molnar, & Wood, 2017); the pathological differences in cardiovascular diseases between species may also be relevant (Varki et al., 2009). However, the association between BMI, a direct anatomical measurement, and the AL factor was the same between species, which suggests that anatomical differences may not be relevant to the pathogenic differences between chimpanzee and human cardiovascular disease. The intercepts of various biomarkers differed as well, but these differences were small compared to the influences of the variables' loadings on AL (e.g., cholesterol: b = 0.520, c = -0.045), and for the variables where intercepts did differ, the differences were not large (e.g. systolic BP: human c = -0.080, chimpanzee c = -0.088).

In both species, our AL measures were strongly associated with age. As AL is defined as an accumulation of the effects of stress over time, this is unsurprising. Nevertheless, with a novel species it is important to verify the validity of the measure. A surprising finding concerned BMI: in chimpanzees, BMI was the only AL biomarker not associated with age, suggesting that some chimpanzees are overweight throughout the course of their lives, while others are not. Why this effect differs from what we observed in humans, where individuals tend to gain weight over time, is an interesting question for future research, but beyond the scope of this study.

With respect to biological sex, female humans are known to have lower AL than males (Juster et al., 2010), but the evidence for this in chimpanzees was not as strong, as there were no statistically significant differences in biomarker levels between sexes. However, a MANCOVA demonstrated that there was no significant species x sex interaction, which we would have expected to find if females had lower AL in humans, but not in chimpanzees. Taking into account all possible interactions within the MANCOVA, including significant age x sex and age x sex x species, might have better explained the group differences we observed between species and sex in Table 5.11.

This study faced several limitations. The chimpanzee sample was taken opportunistically, so we were unable to manipulate what ages measurements were taken at within individuals, and we were also unable to collect biomarkers like interleukin-6 or cortisol. The biomarkers we used appeared to be valid, but the interpretations of a biomarker like phosphate is not as well understood as others (again, e.g., interleukin-6). Whether factor or principal components analyses are viable methods for assessing the structure of biomarkers remains an open question (Crook & Booth, 2017), although the structure of our analyses did not depend on our choice of data reduction method. Similarly, because we wanted to compare the structural composition of an AL factor between species, we did not use cut-points. It is another open question what is the best method for aggregating dysregulation measures over time, and to understand AL in chimpanzees more completely, different aggregation methods (sum scores, weighted sums, binary cut-points) ought to be explored further.

In summary, our results suggest that a meaningful measure of AL can be calculated for individual chimpanzees using physical and blood biomarkers. As individuals age, physiological dysregulation grows and AL increases. That the structures of AL are similar between humans and chimpanzees suggests that the physiological underpinnings of stress have deep evolutionary roots. Future work ought to investigate a greater variety of biomarkers in other primate species such as bonobos and capuchins, and link AL with a wider range of health influences and outcomes. These studies add much to our understanding of captive animal management and the evolution of stress.

6 Personality and allostatic load biomarkers in Japanese and American humans, and chimpanzees

6.1 Introduction

Stress can come from many sources, both environmental and psychosocial, but allostatic load (AL) is affected by virtually all stressors (McEwen, 2000). As described in chapter 5, AL operationalizes the accumulation stress over time, as measured by physiological dysregulation in multiple bodily systems. Over the course of a lifetime, this accumulation can have far-reaching consequences for mental and physical health. Individuals with high AL are physically weaker (Mori et al., 2014), and more likely to become disabled (Juster et al., 2010); they also suffer from higher rates of cognitive decline (Karlamangla et al., 2014) and depression (Kobrosly, Seplaki, Cory-Slechta, Moynihan, & Wijngaarden, 2013). Ultimately, high AL is associated with increased all-cause mortality risk (Seeman, McEwen, Rowe, & Singer, 2001).

While the effects of AL are far ranging, and include psychological outcomes, the impact of psychological variables on AL has come under study as well. Both personality and AL are major predictors of mortality (Roberts et al., 2007; Seeman et al., 1997); moreover, both personality and AL are broad measures with known connections to a myriad of other systems and outcomes. For example, the personality trait of hostility, frequently associated with higher development of CVD (Friedman,

Tucker, & Reise, 1995), is also linked to higher allostatic load (Kubzansky, Kawachi, & Sparrow, 1999). In this way, single personality traits are implicated in the development of multiple disorders, but a single disorder can also result from the effects of multiple distinct vulnerabilities (Beauchaine, Klein, Crowell, Derbidge, & Gatzke-Kopp, 2009), in this case, different dimensions of the FFM.

Of the dimensions in the FFM, Conscientiousness and Neuroticism are the two most frequently associated with biomarkers of health, including metabolic (Human et al., 2013), cardiovascular (Terracciano et al., 2014), and inflammatory (Luchetti et al., 2014) markers. Conscientiousness and Neuroticism are also notable for being associated with mortality (Roberts et al., 2007), mental health (Strickhouser et al., 2017), and health behaviors, particularly non-social behaviors, such as prevalence of smoking or alcohol consumption (Turiano et al., 2015). Focusing on relationships with a multisystem AL construct, high Neuroticism, low Extraversion, and low Conscientiousness tend to have higher AL (Stephan, Sutin, Luchetti, & Terracciano, 2016).

However, the effects of personality on AL are often inconsistent between samples (Allen & Laborde, 2017). This could come down to a range of factors, but culture is possibly the most powerful, least understood of these moderators (Ryff et al., 2015). Investigators are increasingly searching for cross-cultural effects, that is, effects that are or are not the product of differences in cultural environments. If an association is consistent across samples from different cultures, this is strong evidence that the effect is robust. If an association is consistent across cultures and in a closely-related species, such as chimpanzees, then this would be even stronger

evidence for the robustness of the effect. AL has been assessed and studied in many populations (Juster et al., 2010), but the specific relationships between AL and personality, across cultures, has been little studied.

In chapter 4, we established links between Agreeableness and mortality in chimpanzees, and in chapter 5, we explored biomarker data from a chimpanzees, guided by a human dataset. We found that the types of biomarkers that contributed to an emergent AL latent variable were similar between humans and chimpanzees. Some notably differences emerged, for instance, there were fewer significant sex differences in biomarkers among chimpanzees, and BMI appeared not to change with age in chimpanzees. However, the overall findings support the presence of a cross-taxonomic tribe (*Hominini*) AL construct in chimpanzees and humans.

Although AL has been provisionally studied in some nonhuman primates (Edes & Crews, 2017), and personality and mortality has been studied in a few species (Seyfarth et al., 2012; Weiss et al., 2013), only two studies have touched on these issues in chimpanzees. Both examined behavioral measures of personality and cortisol levels in captive chimpanzees, but neither found consistent associations between cortisol levels and personality (Anestis, 2005; Anestis et al., 2006).

American chimpanzees benefit from the advantages of western civilization, but also experience several of the same downsides. Chimpanzees living in captivity in the US tend to lead largely sedentary lives, where food is plentiful, but made from processed materials, and health care is readily available. Of particular note, captive chimpanzees, and indeed all captive great apes, including sedentary humans, suffer from disproportionately high rates of CVD (Varki et al., 2009), compared to wild

chimpanzees (Hill et al., 2001). In these ways, captive chimpanzees' life trajectories resemble those of modern, post-industrial humans.

Personality is posited to be associated with AL through three main paths, as introduced in chapter 1: health behaviors associated with specific personality dimensions, causative influences of personality on physiology, and biological third variables, e.g., common genes. As demonstrated, captive chimpanzee mortality more closely resembles post-industrial human mortality than mortality among wild chimpanzees. Thus, captive chimpanzees provide a powerful means of controlling for the importance of health behaviors. Possessing a similar personality structure to humans (King & Figueredo, 1997) and living in similar environments, chimpanzees differ in a key respect: chimpanzees do not have the ability and do not possess sufficient knowledge to alter their behavior to reduce unhealthy or increase healthy habits. In this way, the captive chimpanzee population allows us to carry out a natural experiment, wherein our chimpanzee sample allows us to control for the effects of health mediating behaviors.

However, human environments vary even between developed nations; cultural differences might also affect how psychology and health are related (Boylan, Tsenkova, Miyamoto, & Ryff, 2017; Miyamoto et al., 2013). For example, Americans and Japanese humans are members of the same species, but captive chimpanzees living in the US arguably share a culture with American humans. Which might be more relevant to the effects of personality on AL, species or culture? To investigate these contrasts, we identified two human samples – the Midlife in the United States (MIDUS) study and the analogous Midlife in Japan (MIDJA) study –

which had a high degree of overlap in variables, and our chimpanzee sample, allowing us to make direct comparisons across groups. To the best of our knowledge, no previous researchers have had access to nonhuman individuals who have been both comprehensively rated for personality and assayed for biomarker levels. In this chapter, we explore the effects of personality on AL, as informed by our examination of AL biomarkers in chapter 5, and compare the chimpanzees to these two distinct, culturally representative samples of humans.

6.2 Methods

6.2.1 Study Subjects

6.2.1.1 American Humans

Personality and biomarker data were drawn from the MIDUS study, which included a subsample in which biomarkers were drawn from select members the MIDUS II sample (Dienberg Love, Seeman, Weinstein, & Ryff, 2010). 993 individuals participated in the MIDUS II biomarker survey.

6.2.1.2 Japanese Humans

The sister project to MIDUS, Midlife in Japan (MIDJA), began in 2008. By design, the variables gathered during the MIDJA study have a high degree of overlap with those from the MIDUS study, including personality, most blood biomarkers, blood pressure, and BMI measurements. 382 individuals participated in the MIDJA biomarker survey.

6.2.1.3 American Chimpanzees

The sample of and data from chimpanzees was the same as that used in chapter 5.

6.2.2 Personality

6.2.2.1 Humans

Both American and Japanese humans were assessed for personality using the Midlife Development Inventory (MIDI), developed in English and translated into Japanese (Lachman & Weaver, 1997). Participants were asked to rate how well 31 adjectives described themselves using a four-point scale ranging from 1 (not at all) to 4 (a lot). The 31 items represent the standard dimensions of the FFM, as well as a sixth dimension, referred to as 'agency' by the MIDI. Agency consists of five items: 'self-confident', 'forceful', 'assertive', 'outspoken', and 'dominant'. Because of the strong conceptual overlap with the chimpanzee Dominance dimension, we referred to agency as Dominance and treated the score as we would a chimpanzee Dominance personality score.

Four items assessed Neuroticism, five items assessed Extraversion, seven items assessed Openness, five items assessed Agreeableness, and five items assessed Conscientiousness. The reliability of the MIDI dimensions in both samples was adequate to strong (Figueredo et al., 2005; Lachman & Weaver, 1997; Sutin et al., 2015).

6.2.2.2 Chimpanzees

Personality was assessed with the CPQ, as described in (Weiss et al., 2007), and elaborated on in the preceding chapters.

6.2.3 Biomarkers

Previous studies have examined many biomarkers in these humans samples (Boylan et al., 2017; Ryff et al., 2015). To maintain comparisons that were as direct

as possible, we analysed only the biomarkers that were shared between all three samples: total cholesterol, triglycerides, BMI, systolic blood pressure (SBP), and diastolic blood pressure (DBP). The details of blood sampling and biomarker collection are available in the MIDUS and MIDJA codebooks, which can be found online on the ICPSR website.

In humans, biomarkers were measured in a single instance for every participant of the MIDUS and MIDJA biomarker studies. In chimpanzees, an average of all measurements for a given biomarker was used, except where indicated. A summary of all variables we analyzed from the MIDUS and MIDJA samples is presented in Table 6.1. Comparable descriptions of all these variables for the chimpanzees can be found in chapters 4 and 5.

Table 6.1

Descriptive statistics for the biomarker subsamples of the Midlife in the United States and Japan studies.

	Japanese (N = 382)		Americans (N = 993)	
Variable	Mean	S.D.	Mean	S.D.
Age	55.47	14.04	58.11	11.69
Dominance	1.87	0.67	2.63	0.74
Extraversion	2.47	0.72	3.14	0.65
Openness	2.23	0.65	3.00	0.68
Conscientiousness	2.66	0.61	3.41	0.53
Agreeableness	2.70	0.68	3.45	0.58
Neuroticism	2.15	0.65	2.05	0.73
BMI	22.58	2.96	29.05	5.91
Cholesterol	205.81	38.21	186.93	40.4
Triglycerides	144.65	113.31	134.98	142.39
Systolic BP	121.64	19.95	130.76	17.76
Diastolic BP	71.06	11.36	74.98	10.14

Note. BMI = Body Mass Index; BP = Blood Pressure. The Japanese sample includes 214 women; the American sample includes 548 women.

6.2.3.1 Corrections for medication use

The chimpanzees living at YNPRC had access to good healthcare, but the targets of medical treatments differed from human populations. Specifically, humans are often treated for heart conditions, which can affect biomarker measurements.

The MIDUS and MIDJA studies recorded the most common medications used to treat CVD and high cholesterol. Relevant to the biomarkers we analysed were blood pressure lowering medications, and statins, which lower cholesterol levels. Individuals taking blood pressure medications had 10 and 5 mmHg added to their SBP and DBP, accordingly (Law, Wald, Morris, & Jordan, 2003). Individuals taking statins had 21.24 mg/dL added to their total cholesterol levels (Law, Wald, & Rudnicka, 2003). All adjustments were made prior to standardization.

6.2.3.2 AL scoring

After standardization, AL scores were calculated by averaging all of an individual's biomarkers. Some individuals were missing data, thus, this did not downward bias the AL scores of these individuals as a straightforward sum-score would.

To achieve this effect in our SEMs, AL was defined as a latent variable composed of equally weighted, standardized (*z*-scored) variables. Full information maximum likelihood estimation was used to account for missing values.

6.2.4 Control variables

Age and sex are frequently included in allostatic load and wider epidemiological studies as control variables. Age^2 is also frequently included in

studies of older individuals to control for the increasing rate of allostatic load accumulation in older age groups. Our models included all of these variables.

6.2.5 Standardization

Where possible, variables were standardized across all three samples. MIDI personality scores ranged from 1 to 4, while CPQ scores ranged from 1 to 7, so the chimpanzees' scores were rescaled to range from 1 to 4, and then all personality dimensions were standardized across the samples. Blood and blood pressure biomarker measurements overlapped and did not appear to differ substantively between the samples (Figure 6.1), so all were standardized across the three groups. The physical dimensions of chimpanzees are considerably different from those of humans, so BMI was scaled within species groups, that is, we standardized the chimpanzees' measurements separately from all of the humans' measurements.

Chimpanzees' life histories are faster than humans. To make age and age^2 variables informative in all group comparisons, we transformed chimpanzee age. The chimpanzee growth rate is approximately 50% faster higher than humans' (Napier & Napier, 1967), thus we multiplied chimpanzee age by 1.5 (King et al., 2008) before also squaring and standardizing across all groups.

6.3 Results

6.3.1 Suitability of data

To check whether the data were suitable for multivariate analyses, we applied Bartlett's test of sphericity to the correlation matrices of each dataset. The MIDUS data ($\chi^2 = 6972$, $p < 0.001$, $df = 91$), MIDJA data ($\chi^2 = 3293$, $p < 0.001$, $df = 91$), and YNPRC data ($\chi^2 = 1535$, $p < 0.001$, $df = 91$) were all indicated to be suitable.

6.3.2 Structural Equation Modelling

Our SEMs featured sex, age, and age^2 as control regression paths, and the Dominance, Extraversion, Conscientiousness, Neuroticism, Agreeableness, and Openness scores as regression paths of interest. As described in the methods, AL was formed by defining it as a latent variable with equal loadings from all of our biomarkers, which had been standardized prior to our analyses.

Because we were primarily interested in species and culture differences, we hypothesized four possible groupings of our three samples:

1. All samples were modelled together, belonging to one group. Parameters were jointly estimated for all personality regressions on AL.
2. Humans vs. Chimpanzees: Regression parameters were jointly estimated for MIDJA and MIDUS, and separately for YNPRC.
3. Americans vs. Japanese: Regression parameters were jointly estimated for MIDUS and YNPRC, and separately for MIDJA.
4. All parameters were estimated separately, each sample belonging to its own grouping.

In all models, age and sex control variables were estimated freely across all three samples. The fit statistics for these models are shown in table 6.2.

Table 6.2

Fit statistics for differently grouped AL and personality models

Model	$\chi 2$	df	CFI	RMSEA	SRMR
1. Joint estimation in all samples	1205	120	0.492	0.132	0.165
2. Joint estimation by species	1199	114	0.492	0.136	0.165
3. Joint estimation by culture	1200	114	0.491	0.136	0.165
4. Free estimation within samples	1193	108	0.492	0.136	0.165

Note. df = Degrees of Freedom, CFI = Comparative Fit Index, RMSEA = Root Mean Squared Error of Approximation, SRMR = Standardized Root Mean Residual

We used the same fit measures to assess our SEMs as in chapter 5: Comparative Fit Index (CFI), an incremental fit index based on model non-centrality; Root Mean Square Error of Approximation (RMSEA), an absolute index based on non-centrality; Standardized Root Mean Residual (SRMR), an absolute index with no penalty for model complexity (Hu & Bentler, 1999).

As indicated by all of these measures, model fit was poor, so the parameter estimates of the model could not be assumed to be reliable. We inspected in the modification indices, which indicated that the best way to improve fit was to free the fixed loadings between the physiological biomarkers and the AL latent variable. To do so would violate the assumption of the model, which fixed the loadings of the biomarkers so comparisons could be made across samples.

6.3.3 Linear Regression Modelling

Since the model fits of our SEMs were poor, we could not be confident that we could trust the parameter estimates or statistical tests which resulted from our

analyses. Thus, to compare the effects of personality on AL across the three samples, we shifted to a simpler, linear modelling approach.

We built three separate models, one for reach sample. In the human samples, AL scores were predicted using general linear models. In chimpanzees, because we had multiple measurements of biomarkers from each individual, we used mixed models to introduce a random effect for the individual, which is a more powerful method than averaging the measurements (Robinson, 1991) as we did in chapter 5. Introducing a random effect for an individual adds an extra term to the linear regression equation that essentially modifies the intercept. The equation differs for each individual, so all observations from the same individual will have the same intercept, which is a different from other individuals' intercepts. A general intercept term for the equation still exists, but the random effect modifies the intercept value from the starting point that is the general intercept. The term is called random because it is uncorrelated with the independent variables. Despite differences in estimation approach, regression coefficients between linear and linear mixed models are directly comparable when mixed model coefficients are calculated using maximum likelihood estimation, as opposed to restricted maximum likelihood estimation (Oehlert, 2014). All three models contained the same predictors (Table 6.3).

Our models reveal close consistency between the human samples. The dominant demographic variables, sex, age, and age^2, all had similar estimates in Americans and Japanese, though in the chimpanzee model, none of these variables were significant. The impact of personality was not as strong as demographics, but

we nevertheless found a positive relationship between Agreeableness and AL in both human groups. Americans also exhibited a negative relationship between Conscientiousness and AL. The chimpanzee sample did not reflect any of these effects, but revealed only a positive relationship between Dominance and AL.

Table 6.3

Results of linear regression models of AL and personality

	Japanese			Americans			Chimpanzees		
Variable	*B*	95% CI		*B*	95% CI		*B*	95% CI	
(Intercept)	0.39	[0.20,	0.58]	0.40	[0.28,	0.52]	-0.10	[-0.43,	0.22]
Sex	**-0.35**	**[-0.47,**	**-0.24]**	**-0.25**	**[-0.33,**	**-0.18]**	0.10	[-0.10,	0.29]
Age	**1.25**	**[0.73,**	**1.79]**	**1.08**	**[0.69,**	**1.48]**	-0.03	[-0.69,	0.64]
Age^2	**-1.00**	**[-1.52,**	**-0.48]**	**-0.98**	**[-1.34,**	**-0.62]**	0.19	[-0.47,	0.84]
Dominance	0.07	[-0.01,	0.14]	0.03	[-0.01,	0.08]	**0.14**	**[0.03,**	**0.26]**
Openness	-0.04	[-0.13,	0.04]	-0.03	[-0.07,	0.02]	0.00	[-0.12,	0.13]
Agreeableness	**0.10**	**[0.02,**	**0.18]**	**0.06**	**[0.02,**	**0.11]**	0.03	[-0.10,	0.15]
Conscientiousness	-0.00	[-0.07,	0.07]	**-0.04**	**[-0.08,**	**-0.01]**	0.11	[-0.03,	0.25]
Neuroticism	-0.05	[-0.12,	0.01]	0.03	[-0.01,	0.06]	-0.04	[-0.16,	0.08]
Extraversion	-0.04	[-0.12,	0.05]	-0.01	[-0.06,	0.04]	-0.12	[-0.28,	0.05]

Note. Variables whose confidence intervals do not overlap with 0 are shown in bold.

Finding an association between high Agreeableness and high AL and poor health was unexpected (Stephan et al., 2016), but in the MIDUS sample, similar analyses were able to explain some of this effect by including an interaction between Agreeableness and Conscientiousness in regression models of mortality: individuals who were highly agreeable and highly conscientious tended to live longer (Chapman, Fiscella, Kawachi, & Duberstein, 2010). Since we were using the exact same MIDUS data, and the same scales and biomarker measures in the MIDJA, we added an Agreeableness x Conscientiousness interaction to all of our models and refit them. In none of our models did the inclusion of this interaction improve the fit of the model (Table 6.4), nor did it greatly affect any of estimates of the other variables.

Table 6.4

Comparison of models with and without Agreeableness x Conscientiousness

	Japanese			Americans			Chimpanzees		
Variable	LL	df	AICc	LL	df	AICc	LL	df	AICc
Without A x C interaction	-314.6	11	651.8	-814.5	11	1651.2	-400.9	12	826.6
Including A x C interaction	-314.1	12	653.1	-814.4	12	1653.1	-400.0	13	826.9

Note. LL = log-likelihood, df = degrees of freedom, AICc = corrected Akaike Information Criterion

6.4 Discussion

In these analyses of three samples with similar variables on demographics, personality, and allostatic load, we found significant relationships between personality and allostatic in all samples. However, the relationships between personality and AL were consistent between the American and Japanese human samples, but these similarities did not extend to the sample of American chimps.

These results are evidence that the relationships between personality and AL differ between species, and not strongly determined by cultural factors.

What do these contrasts tell us about the mechanisms that drive the associations between personality and AL? By studying captive chimpanzees and comparing them with modern post-industrial humans, we were able to rule out many third variables, which could be giving rise to individual differences in personality and AL, and in particular, variables which are environmental, such as diet, and availability of modern medicine and health-care.

The other main class of biological third variable is genetics. Personality is known to be heritable in both humans (Bouchard & Loehlin, 2001; Jang, Livesley, & Vemon, 1996) and chimpanzees (Weiss et al., 2000; Wilson et al., 2017), and in humans, personality has been genetically linked to several mental and physical disorders (Gale et al., 2016), as well as broader measures of health (Figueredo, Vásquez, Brumbach, & Schneider, 2004). Of note, subjective well-being, which is positively correlated with health and lower risk of mortality (Diener & Chan, 2011; Okun et al., 1984), is genetically correlated with personality in humans (Weiss et al., 2008), chimpanzees (Weiss, King, & Enns, 2002), and orangutans (Adams, King, & Weiss, 2012). Considering the high levels of similarity in personality, genetics, and even genetic correlations between humans and chimpanzees, we do not believe that genetic third variables are a substantial source of difference in the relationships between AL and personality in humans and chimpanzees.

For much of the same reasons that we do not believe that differing genetics could play a role as a third variable, the evidence does not support an explanation in

which personality has different direct effects on health, which might vary by species. Again, humans and chimpanzees are very closely related and the ways in which chimpanzees and humans differ from a biomedical perspective largely have to do with susceptibility to infectious diseases (Olson & Varki, 2003). This is consistent with the most rapidly diverging gene clusters between humans and chimpanzees, which are predominantly immunological, sensory, and epidermal (Chimpanzee Sequencing and Analysis Consortium, 2005). Moreover, as shown in chapter 5, the biological markers of AL, the system in question, are remarkably similar in humans and chimpanzees. For all these reasons, it is unlikely that the relevant physiological systems differ between humans and chimpanzees. It is also unlikely that these systems in humans and chimpanzees living in the same environments would be differently effected by personality.

Our results are consistent with the behavioral account of the relationship between personality and health (Turiano et al., 2015). For example, high Conscientiousness humans tend to engage in healthier behaviors: they smoke less, drink less, and exercise more. 42% of the association between Conscientiousness and mortality was mediated by health characteristics in the MIDUS sample. As also shown by the MIDUS sample, these individuals have lower AL. High Conscientiousness chimpanzee do show remarkably similar behaviors to humans, as described in chapter 2, but captive chimpanzees simply do not have the ability to engage in health promoting behaviors, at least not to nearly the same extent as humans.

However, while chimpanzees do not engage in the same behaviors as humans regarding health habits, this does not mean that chimpanzees do not engage in personality-linked behaviors that affect their health. Chimpanzees rated high in Dominance engage in more aggressive, confrontation behaviors (Pederson et al., 2005), such as displaying, intervening, and copulation (Freeman et al., 2013). These are stressful, often high-risk behaviors. Much has been written on the effects of Dominance on stress, health, fitness, and longevity (Sapolsky, 1994, 2004), and this research has largely been conducted in the wild. That Dominance remains the crucial personality variable for predicting captive chimpanzee stress, via AL, suggests that captive chimpanzees are engaging in the same health affecting behaviors as wild chimpanzees, but humans no longer share these behaviors with our closest evolutionary relatives. It could be that with regards to AL, humans more closely resemble our other closest relative, the bonobo. Bonobos are notable for having less violent, matriarchal societies (Stumpf, 2007), though their personalities are similar to those of humans and chimpanzees (Weiss et al., 2015), so comparable personality relationships could be investigated if AL data were available for bonobos.

The effect of Dominance stands in contrast to our findings in chapter 4, where we found no effect of Dominance on longevity in captive chimpanzees, but did find a protective effect of Agreeableness. AL is known to be associated with mortality in humans (McEwen & Seeman, 1999); this study was unable to test this association in chimpanzees, but given the consistency in AL structure found in chapter 5, it is unlikely that AL is not related to lifespan in chimpanzees as well. Why, then, did we not find similar associations with chimpanzee personality in chapters 4 and 6? It may be that while AL is associated with mortality risk, enough

variation exists that personality differences could emerge between individuals who at high risk of dying and individuals who experience more stress over their lifespan. Additionally, the issues of age confounding that became apparent in chapter 4 could also be affecting these analyses, even though they are not survival analyses. Another possible explanation is that we did not possess sufficient power to detect the effects of Agreeableness in this study or Dominance in chapter 4. To the best of our knowledge, there is no precedent for this sort of study in chimpanzees, so any estimate of an effect size is not likely to be accurate.

With respect to human Agreeableness, our results are unusual in that high Agreeableness, which is widely associated with good health (Strickhouser et al., 2017) and positive life outcomes (Roberts et al., 2007), was associated with high AL, and consequent poor health, in both of our human samples. There are several possible reasons for this. As mentioned, there is evidence for a protective effect of an Agreeableness x Conscientiousness interaction on mortality (Chapman et al., 2010), but we found no evidence to support the effect of any such interaction in any of our samples. Sensitivity analyses previously demonstrated that the Agreeableness association with mortality is eliminated by controlling for age. This is consistent with Stephan et al. (2016), who found that a 4-year decrease in Agreeableness was associated with higher AL. However, we controlled for both age and age^2 in our models, and yet in these human samples the effect persists. A final caveat to, and possible explanation for, these results lies in the scales themselves. The MIDI composite for Agreeableness has poor convergent validity with the Agreeableness domain from the NEO short form (0.42), while also being significantly correlated with both Extraversion (0.38) and Conscientiousness (0.27) on the NEO short form

(Lachman, 2005). Overlap with other personality domains could bias the estimates in regression models one or way or other, though with several issues in play, it is very difficult to determine the impact that the lack of quality in MIDI Agreeableness may have had.

Whatever the reason, it seems clear from our results and repeated demonstrations in earlier studies with the MIDUS (Chapman et al., 2010; Turiano et al., 2015) that the MIDI Agreeableness measure is associated with poor health. We note that, to best of our knowledge, the MIDI Agreeableness measure has not previously been used to assess health in the MIDJA sample, so our finding adds additional credence to the idea that MIDI Agreeableness is tapping into some aspect of negative health, which Agreeableness is not usually associated with (Jokela et al., 2013; Jokela, Pulkki-Råback, Elovainio, & Kivimäki, 2014). Considering the constituent items of MIDI Agreeableness - 'warm', 'sympathetic', 'softhearted', 'caring', and 'helpful' – the origins are likely in social behavior. Whatever these particular behaviors are, they appear to have consistent effects across human cultures.

Another possible explanation for this abnormality is that the effect may be driven from the opposite direction. That is, unhealthy individuals' personalities may change, their poor health may make them less happy, and lower their Agreeableness. However, this explanation suffers from the same issues as the previous account, notably, why has this effect been disproportionately found with the MIDI instrument and not with other measures of Agreeableness? These weakness in both explanations highlights the danger in inferring a causative explanation for the association between

Agreeableness and AL. Further research is required to understand the mechanisms and true direction of these effects.

Although a naturalistic experiment can never control for all confounding variables, and certainly not for all the differences between two species, no matter how closely related they are, our results nevertheless have clear implications. Chimpanzee stress is related to Dominance, which is consistent with the large body of work on hierarchy and health in wild primates (Sapolsky, 2005). Dominance is not normally studied in human systems of personality because it does not naturally emerge from comprehensive human personality data (Latzman, Sauvigné, & Hopkins, 2016). This change in human personality is consistent with our finding no effect of Dominance in the human samples. Instead, Agreeableness appears to be the most important personality variable associated with this measure of human physiological stress, which likely reflects major changes in social organization that have occurred since humans diverged from chimpanzees.

Additional work is necessary, therefore, to understand the mechanisms that link Dominance and Agreeableness to stress, in chimpanzees and humans, respectively. It seems most likely that specific behaviors are at work, as they have been found to be for Conscientiousness (Turiano et al., 2015) but corresponding behaviors have not been identified for Agreeableness or Dominance. Future comparative studies will benefit from the vast existing literature on psychosomatic health, but to understand the evolution of psychosomatic health, more samples must be collected, most importantly, in species other than chimpanzees and humans.

7 Summary and general discussion

This thesis had two main lines of investigation: the associations between primate personality and cognition, and the associations between personality and health. These investigations centered on chimpanzees, though two other highly studied primate species were also examined: rhesus macaques and humans.

The opening chapter of this thesis presented a brief overview of the history and development of the conceptual frameworks for the study of primate personality, cognition, and health, particularly within the field of psychology. In following empirical chapters, we took a broad view to understanding how personality, cognition, and health relate to one another. Based on the results presented in these chapters, we concluded that many meaningful associations exist between personality, cognition, and health, some expected and some unexpected, or at least, not predicted. A summary of our findings is presented in Table 7.1.

As such, personality assessments are a useful technique for understanding how and why individual primates' cognitive abilities and health outcomes differ. This final chapter discusses the findings of the present thesis, highlights notable limitations of our work, and offers some recommendations and implications for future research.

Table 7.1

Summary table of major findings on personality from empirical chapters

Chapter	Species	Conscientiousness	Agreeableness	Extraversion	Openness	Dominance	Neuroticism
2	Chimpanzee	Less likely to drop out; learn tasks better.	More likely to drop out, less engaged with tasks.	Faster RTs.	Faster RTs; higher accuracy, more interest in participating.	Slower RTs.	None.
3	Macaque	No comparable dimension.	Higher overall performance after learning a list; slower RTs.		Faster list acquisition; faster RTs.	Slower RTs.	None.
4	Chimpanzee	None.	Lower mortality in male chimpanzees	None.	Lower mortality in female chimpanzees	None.	None.
6	Chimpanzee and Human	Lower AL in American humans.	Higher AL in humans.	None.	None.	Higher AL in chimpanzees.	None.

Note. Chapter 5 has been omitted from this table as it contains no results pertaining to personality. In chapter 3, Agreeableness and Extraversion are merged to reflect the overlap that macaque Friendliness has with these two dimensions.

7.1 Insights into chimpanzee personality

7.1.1 Conscientiousness

Conscientiousness is not frequently identified in factor or component models of primate personality (Freeman & Gosling, 2010), but studies that have used comprehensive questionnaires have found Conscientiousness in chimpanzees (Freeman et al., 2013; King & Figueredo, 1997; Weiss, Inoue-Murayama, et al., 2009). In chimpanzees and primates more generally, Conscientiousness tends to be lost among other dimensions of personality, such as Freeman et al.'s (2013) 'Reactivity-undependability' and Massen et al.'s (2013) 'Exploration-persistence'. Nevertheless, a recent meta-analysis of the animal personality literature suggests that distinct aspects of Conscientiousness can be found in many other primate and nonprimate species (Delgado & Sulloway, 2017).

As Conscientiousness is infrequently identified, there have been comparatively few attempts to study it, even exploratorily. In a study correlating the CPQ to behavior among a sample of zoo housed chimpanzees, Conscientiousness was linked to reduced occurrence of aggressive displays and no other behaviors (Pederson et al., 2005). In the study that extracted 'Reactivity-undependability', that dimension was associated with higher rates of sexual behavior, social intervention, and less post-conflict aggression (Freeman et al., 2013). However, this dimension mixes items normally associated with Dominance and Neuroticism, in addition to Conscientiousness, so it is difficult to conclude which of these behaviors might specifically be related to chimpanzee Conscientiousness.

In this light, chapter 2 greatly expands our understanding of chimpanzee Conscientiousness. Our results demonstrate that in the context of experimental testing, more Conscientious chimpanzees will participate in testing for longer, dropping out less, across multiple phases of an experiment. These individuals perform better on average, but this can be explained by their greater experience. Conscientiousness was also associated with other variables like response time and number of touches to the screen per trial, and these associations fit with our understanding of Conscientiousness as a measure of dependability and self-control (King & Figueredo, 1997).

We did not find any associations between chimpanzee Conscientiousness and either mortality or AL. According to the behavioral hypothesis of personality and health, high Conscientiousness individuals engage in more health promoting behaviors (Hagger-Johnson & Whiteman, 2007), such as taking prescribed medication and abstaining from drinking alcohol. This is reflected in chapter 6, where we found an association between high Conscientiousness and low AL in the MIDUS sample. Chimpanzees do not drink alcohol and medication is administered to them so that they do not have a choice in the matter. Thus, it is not surprising that we found no associations between Conscientiousness and health in chimpanzees given that the effects of Conscientiousness are known to be mediated by specific behaviors (Turiano et al., 2015). Our findings serve to bolster the behavioral explanation for the Conscientiousness-mortality link.

On the other hand, all of the chimpanzees under study lived in captivity, and in a captive setting, chimpanzees may not be able to exercise their conscientious

tendencies to the fullest. For example, wild chimpanzees are known to eat specific plants for the purposes of self-medication (Huffman, 1997); high Conscientiousness individuals might be more diligent about seeking out and consuming these plants in the wild, but if they do not have access to medicinal plants in captivity, then the association would not be reflected in captive data.

7.1.2 Agreeableness

Agreeableness was found to play a number of important roles in several of our studies. This was somewhat unexpected, as Agreeableness is not typically associated with cognitive abilities or intellectual achievement in humans (Chamorro-Premuzic & Furnham, 2006). Nevertheless, we found that high Agreeableness chimpanzee were more likely to drop out of testing and less likely to be engaged in testing. In the social setting of these tasks, it is tempting to suggest that the high Agreeableness chimpanzees were more deferential to other chimpanzees, the thus the low Agreeableness individuals spent more time interacting with the touchscreen. However, this is essentially describing Dominance, not Agreeableness.

As discussed in the context of Conscientiousness, two studies have looked at the behavioral correlates of chimpanzee personality dimensions. One found that high Agreeableness was associated with fewer aggressive displays and more solitary grooming (Pederson et al., 2005), while the other found Agreeableness to be associated with fewer displacing actions and more general affiliative behavior (Freeman et al., 2013). The items that constitute chimpanzee Agreeableness – 'sympathetic', 'helpful', 'sensitive', 'protective', 'gentle', and 'conventional' – have also been described as 'altruistic' (Weiss, Adams, Widdig, et al., 2011). A better

explanation for high Agreeableness chimpanzees' lack of interest in the task might be that in this social setting, these chimpanzees were more interested in affiliating with and being around conspecifics. Low Agreeableness individuals, less interested, were likely less inclined to care about the presence or interests of the other chimpanzees.

As discussed at the end of chapter 3, macaque Friendliness incorporates aspects of both Agreeableness and Extraversion. In particular, individuals rated higher on 'helpful', 'sensitive', and 'sympathetic' tended to perform better on the serial cognition tasks. These item level associations were consistent, but not especially strong. However, these associations are the opposite of the associations we observed between Agreeableness and performance in chimpanzees. Inconsistencies at several levels indicate that further investigation is required to understand the associations between Agreeableness and cognition.

With regards to health, our results agree with much of the literature. Although Agreeableness is not as consistent a predictor of mortality in humans (Jokela et al., 2013), there do appear to be relationships between Agreeableness and both mental and overall health (Strickhouser et al., 2017), and studies which used more comprehensive assessments of Agreeableness found that Agreeableness and its facets were consistently associated with longevity (Costa, Weiss, Duberstein, Friedman, & Siegler, 2014; Weiss & Costa, 2005). Notably, these studies did not divide their samples by gender, so we cannot discuss whether there are specific sex based effects of personality on longevity, as we found in chapter 4. The associations between Agreeableness and longevity in chimpanzees did not appear to extend to AL.

7.1.3 Extraversion

Extraversion, like Agreeableness, is primarily a social dimension of personality: Extraversion represents how frequently an individual engages in social interaction, whereas Agreeableness represents how well an individual interacts with others (Wilt & Revelle, 2008). Again, somewhat surprisingly, Extraversion was found to be important in our cognitive experiments, but not in our studies of health.

Extraversion was related to higher accuracy in study 1 of chapter 2, and associated with faster response times in studies 1 and 2, suggesting a link between Extraversion and cognitive abilities, particular motor processes such as those involved in processing time. Extraversion was not positively related to interest or participation in the computer tasks during these studies. However, reflecting Extraversion's measure of sociality, when free rewards were available in the research pods and many chimpanzees entered and stayed in the pods to forage, those who spent the longest amount of time in the pods, around other chimpanzees, were higher in Extraversion.

In addition to the adjectives discussed in the previous section on Agreeableness, specific items of macaque Friendliness which were related to performance were 'decisive', 'sociable', 'persistent', and 'intelligent', where the description of intelligence specifically defines it as a measure of social intelligence. The mix of Friendliness items that associate with performance make it difficult to further deconstruct what particular aspect of macaque social personality are markers for high performance in the context of the non-social testing setting of chapter 3.

Sociality has been linked to longevity in other primates (Brent, Ruiz-Lambides, & Platt, 2017; Silk et al., 2010), and Extraversion specifically has been linked to greater longevity in captive gorillas (Weiss et al., 2013). In light of the similarities between that sample of gorillas and our sample of chimpanzees, it was surprising that we did not find an association between Extraversion and longevity in captive chimpanzees. Chimpanzees' dynamic fission-fusion social system (Aureli et al., 2008), compared to gorillas' stable harem system (Robbins, 1999), may go some distance to explaining why Extraversion does not relate to longevity the same way between these two species.

In many species (Goymann & Wingfield, 2004), AL is frequently linked to rank and social status (see Dominance, below), and in humans, AL is associated with many aspects of the social environment, though these associations change with age (Brooks et al., 2014). Specifically, low Extraversion and declines in Extraversion were related to higher AL (Stephan et al., 2016). We did not observe any associations between Extraversion and AL in either human sample, or the chimpanzee sample. This could be due to basic sample differences or lack of statistical power, as well as several other factors. Our study used slightly different biomarkers to operationalize AL; we did not have access to more specific markers such as glycated hemoglobin and C-reactive protein. Without some of the more commonly used biomarkers, we may have found less strong associations, or not had sufficient power to detect as many associations. However, the association we did find are likely to be more generalizable.

On the other hand, both Brooks et al. and Stephan et al. used the Midlife Development Inventory, which was designed for and used in both the MIDUS and MIDJA studies, though our study is one of the few to use the inventory's unique measures of Dominance, which in the FFM is incorporated into Extraversion (McCrae & Costa, 1989).

7.1.4 Openness

Openness has been frequently linked to interest and participation in studies of animal personality and cognition (Herrelko et al., 2012; Massen et al., 2013; Morton, Lee, & Buchanan-Smith, 2013), a finding which we replicated in chimpanzees. Less clear evidence has been advanced that Openness also relates to intelligence in primates (Hopper et al., 2013). Chapters 2 and 3 suggest that Openness is related to performance, both accuracy and response time, in both chimpanzees and macaques. The associations were generally reliable, but not exceptionally strong. This suggests that Openness taps into an aspect of intelligence across primate species.

Moreover, chimpanzees that score higher on Openness appear to be more interested in experimental tasks. This preference cannot be purely explained by a desire to maximize rewards, for as we demonstrated in chapter 2, chimpanzees higher in Openness spent more time with the experimental apparatus, even when the apparatus did not give out any rewards. Some aspect of participating in experiments is inherently desirable for high Openness chimpanzees.

Openness is not typically associated with health, despite being associated with general intelligence, which is strongly related to overall health and longevity (Calvin et al., 2011). We found only one association between Openness and health:

female chimpanzees with higher Openness lived longer. This finding is consistent with the theory that higher Openness is selected for in captive populations (Smith & Blumstein, 2008).

7.1.5 Dominance

In factor and component models of chimpanzee personality, Dominance repeatedly emerged first, with the highest eigenvalue (King & Figueredo, 1997; Weiss et al., 2007; Weiss, Sutin, et al., 2009). Despite not emerging as an independent dimension of personality in humans, distinct Dominance-like personality dimensions are found in orangutans (Weiss et al., 2006), bonobos (Weiss et al., 2015), gorillas (Gold & Maple, 1994), macaques (Adams et al., 2015; Weiss, Adams, Widdig, et al., 2011), and brown capuchins (Morton, Lee, Buchanan-Smith, et al., 2013).

All-together, this evidence suggests that Dominance is an important dimension of personality for primates. It was thus not surprising to find that Dominance is associated with higher AL in chimpanzees, which confirms the theories of Goymann and Wingfield (2004): being a high ranked chimpanzees has more costs associated with it than being a low ranked chimpanzee, thus high ranking individuals experience more stress and have higher AL. Every social challenge will likely cause a physiological deviation from homeostasis in the challenged chimpanzee. Dominant individuals frequently initiate displays of physical prowess and respond to others' aggression with displays of their own and even physical contact. While minor displays may have almost zero effect on AL, more significant social conflicts will activate the stress response and increase AL. Dominance, as a

personality dimension, does not necessarily measure rank, but earlier work (Freeman et al., 2013; Pederson et al., 2005) as well as our own results suggest that higher Dominance chimpanzees do indeed assume a higher rank in their social groups.

On the other hand, Dominance was not associated with longevity in captive chimpanzees. We would expect more stressed individuals to die younger, but it appears that AL, at least in so far as it is influenced by Dominance, does not lead to early mortality.

In the cognitive testing settings of chapters 2 and 3, we found little influence from Dominance. In our experiments with chimpanzees, higher Dominance individuals were more likely participate in the first series of experimental tasks. This is likely due to the uncontrolled social setting of the research areas: higher Dominance individuals have greater agency to go where they wish and participate to the fullest extent that they desire. These results are consistent with our findings relating Agreeableness and participation. However, this effect did not extend to studies 2 and 3. However, we did find a positive association between Dominance and response time, although only in study 2.

In our experiment with macaques, Dominance did not appear to be relevant to any of our models of accuracy. We did find a positive association between Dominance and response times, i.e., higher Dominance individuals were slower to respond. It should be noted that in those models, most personality variables that were included in the best fit models were significant. It is understandable that we would not find many associations between Dominance and performance in this study, as we

eliminated all social components, and our task directly tapped into the cognitive representation of serial information (Jensen et al., 2013).

Nevertheless, the response time findings between species match, suggesting that higher Dominance individuals may be less pressured to act quickly, in both social and non-social settings. This implies that Dominance is tapping into an underlying cognitive ability which is drawn out during testing, such as processing speed (Kail & Salthouse, 1994).

7.1.6 Neuroticism

This research found little evidence for a role of Neuroticism in performance or health. This was not especially surprising among our studies of cognition – a previous study with the Edinburgh Zoo chimpanzee sample suggested that Neuroticism was associated with higher vigilance and more self-directed behaviors during research (Herrelko et al., 2012), but this did not impact interest research in that study, nor did it appear to relate to performance in ours.

However, we were surprised not to find associations between Neuroticism and either mortality or AL in chimpanzees. In humans, Neuroticism is frequently linked to poorer health (Strickhouser et al., 2017). In the sample of Japanese chimpanzees, Neuroticism was strongly linked to subjective well-being (Weiss, Inoue-Murayama, et al., 2009), although the American zoos sample did not find this association (King & Landau, 2003). The absence of a Neuroticism effect on either mortality or AL suggests that while there may be greater psychological impacts for high Neuroticism chimpanzees, it does not appear to be associated with physical health.

On the other hand, a Neuroticism effect may have been too weak to detect with our sample. For example, in chapter 6, our slightly unusual AL construct may not have strongly overlapped with health factors related to Neuroticism. After all, we did not find an association between AL and Neuroticism in either human sample. Ultimately, given the lack of associations, we are limited to speculation.

7.2 Limitations and open questions

The interpretation of this work is limited by a number of drawbacks. First, our studies of cognition used 19 and 9 chimpanzees and macaques, respectively. As our power analyses show, when an adequate number of trials are collected, even a smaller pool of subjects can yield meaningful, significant results in differential research. However, simply increasing the number of trials is not a panacea for having a small number of subjects. Studies that use small samples are more susceptible to the influence of extreme observations (Cohen, 1990), and mixed modelling requires random effects structures which in principle should be maximal (Barr, Levy, Scheepers, & Tily, 2013), but in practice maximal models often do not converge (Bates, Kliegl, Vasishth, & Baayen, 2015). Larger sample sizes and both conceptual and direct replication efforts are necessary to corroborate our findings.

Our studies of health are considerably better powered, e.g. in chapter 4, we determined that we possessed a mean power of 0.88, above the gold standard of 0.8. However, associations between personality and health are often modest (Roberts et al., 2007) and effect sizes may be inflated (Ioannidis, 2008). As such, we may not have been able to detect some effects with our samples. These issues are especially salient for difficult to model variables like AL (Crook & Booth, 2017).

Our studies of cognition were also limited by our choice of tasks. The 2AFC, DMTS, and SimChain paradigms are all widely used, but we did not assess all cognitive faculties with our implementations of these paradigms. For example, all of these paradigms are equipped to assess different and overlapping aspects of numerical cognition (Brannon & Terrace, 1998; Jordan & Brannon, 2006; Shepherd, Hautus, & Hutchinson, 2008), but we did not have an opportunity to test this across the entirety of either nonhuman primate sample.

Chapters 2 and 3, while producing complementary results, do not directly overlap. Personality was collected via expert ratings in both studies, but the structure of personality differs between macaques and chimpanzees. Although many analogous dimensions are present, the presence of macaque Friendliness, a mixture of items which in chimpanzees load on Extraversion and Agreeableness, exemplifies the issues with direct comparisons when personality dimensions do not neatly align.

The cognitive tasks themselves also differed, and while all cognitive tasks vary in the extent to which they are *g*-loaded, our results do not suggest that these cognitive tasks lack meaningful associations with intelligence. Nevertheless, the broader structure of the primate intelligence domains requires further investigation in the context of individual personality differences.

The setting and subjects under study in chapters 2 and 3 also differed. In chapter 2 we had little control over the testing environment, in particular, we could not manipulate any social variables. Under the best of circumstances, these variables ought not to affect our results, but might inject noise into our results. Since we were evaluating the effects of personality, including social dimensions of personality,

social variables would be controlled for, to an extent. At very least, the associations we found between personality and participation are informative. However, in chapter 3 we had much greater control over the testing environment, and still found associations between performance and both Openness and Friendliness. While this suggests that the similar effects we found in chapter 2 were not solely attributable to the environment, some environmental and social factors were no doubt in effect, and we are unable to entirely tease apart the influences of internal and external variables in chapter 2.

In our direct comparisons of personality and health, we were able to maintain control over our selections of biomarkers in both chimpanzee and humans, so that exactly the same demographic, physical, and physiological variables were included in our models. However, while the personality dimensions we used were the same on the surface, they differed between humans and chimpanzees in several ways.

All three samples in chapter 6 contained data for us to construct six analogous dimensions of personality. Constructs of personality do not need to use the same items to tap the same underlying psychological substrates (Donnellan, Oswald, Baird, & Lucas, 2006), but this is not guaranteed. Steps must be taken to ensure that inventories overlap.

In the case of the MIDI, several dimensions, notably Agreeableness, do not display good convergent validity with Agreeableness as measured by the NEO short form (Lachman, 2005). Of the MIDI Agreeableness items, 'warm' is more often associated with Extraversion, and in factor analyses of the MIDUS data, it loads on both Agreeableness and Extraversion (Iveniuk, Laumann, Waite, McClintock, &

Tiedt, 2014). Thus, the personality dimensions we used for analyses with the MIDUS and MIDJA data may not represent the big 5 personality dimensions especially well.

This might not be an issue if we wished to only compare MIDI personality scores. However, we also wished to compare MIDI and HPQ scores, and while some items overlap between the MIDI and the HPQ, there are issues in making direct comparisons. For example, take Agreeableness again. HPQ Agreeableness is composed of 'sympathetic', 'helpful', 'sensitive', 'protective', 'gentle', and 'conventional'. MIDI Agreeableness is composed of 'helpful', 'warm', 'softhearted', 'caring', and 'sympathetic'. Of these items, 'helpful' and 'sympathetic' overlap, but even at this level, the overlap is not perfect. The HPQ asks for a rating between 1 and 7, and provides two or three sentences of explanation (King & Figueredo, 1997; Weiss, Inoue-Murayama, et al., 2009), whereas the MIDI presents the word and asks the individual how well the adjectives describes them on a scale from 1 to 4 (Zimprich, Allemand, & Lachman, 2012).

As mentioned above, personality theory indicates assessment can be robust to these sorts of issues. Thus, these differences will not necessarily affect our results, but they do limit our ability to compare results between species. Between the human MIDUS and MIDJA samples, there were linguistic differences, and there may be different connotations to equivalent words in English and Japanese. These differences may actually be captured by the cultural influences we hypothesized in chapter 6, and in this light, discrepancies in meaning are not an issue. Moreover, in chapter 6, our results from the two human cultures were quite similar, suggesting that cultural and linguistic differences may not play a major role studies of these

particular variables. Ultimately, without a detailed linguistic analysis of the translations from English to Japanese, for both the MIDI and HPQ, further interpretation of cultural differences is limited.

Issues may have arisen from chimpanzee personality being other-assessed, while human personality was self-assessed. In principle, other and self ratings do not yield substantially different results (McCrae & Costa, 1987), but this difference could have altered results when viewed in conjunction with other sources of variation.

With regard to biomarkers and AL measures, our decision to use the same biomarkers in all compared samples is a strength, but we must acknowledge issues inherent in any attempt to measure AL. Sum scoring, used in chapter 6, is one method for aggregating AL, but there are many others. We have no reason to believe that our results would change significantly if we calculated AL using a different method, for the many AL scoring systems generally have good convergent validity with one another (Edes & Crews, 2017).

Yet at the core of the AL concept is the assumption that AL is not measuring a single system within an organism, but integrity across systems within the organism. The complex interrelations within and between systems poses problems, for example, BMI, a metabolic marker, is known to have causative effects on other markers, such as blood pressure, a cardiovascular marker (Millard et al., 2015). Complex network relationships such as those observed between physiological biomarkers can produce observed correlations between variables, which factor

analytic methods will be affected by, even though the correlated variables do not have a common cause (Crook & Booth, 2017).

We sought to ameliorate these concerns by using sum scores rather than factor or component scores, in chapter 6. The models we used in chapter 6 were derived from structures developed in chapter 5, where we used PCA for our exploratory analyses, though compared the results with EFA to find negligible differences. In our confirmatory analyses, we used CFA, which was not ideal, given the issues noted in the previous paragraph, but not unjustified given the limitations of contemporary analytic methods and the current standards in the field (Wiley, Gruenewald, Karlamangla, & Seeman, 2017).

Our analyses of AL physiology confirmed an anthropocentric structure of biomarkers. Humans and nonhuman primates have shown the same types of associations between physiological and external stress variables (Edes & Crews, 2017), although previous studies generally have not had access to the number of subjects and biomarkers at the same time, as we had access to in our sample. We would not expect to see major underlying physiological differences between chimpanzees and humans, but small differences may exist, and our analyses were not designed to capture them. Further analyses of this biomarker sample, and ideally, others like it, could answer questions intended to assess specific differences, rather than similarities.

7.3 Future Directions and Conclusions

The future is promising for personality research in chimpanzees and other nonhuman primates. Personality has been shown to be a meaningful predictive tool,

in this thesis and in other research. For example, Capitanio, Blozis, Snarr, Steward, and McCowan (2017) found that female rhesus macaques with similar personalities were more likely to be successfully pair-housed. Additionally, personality traits are associated with self-injurious behavior in chimpanzees (Herrelko et al., 2012). This work demonstrates that chimpanzee personality is related to interest in and performance with research tasks, which may be of use to experimental psychologists who work with chimpanzees or macaque. Our work also shows that chimpanzee Agreeableness and Openness are related to mortality, and Dominance is related to stress; both of these outcomes are of interest to those who work in captive management with chimpanzees. Thus, this thesis meaningfully contributes new applications for the use of primate personality measures in captivity.

In application, personality-health or personality-cognition associations should nonetheless be independently verified for every species. This thesis focused on chimpanzees, which, along with humans, are two of the most studied of all primates. Rhesus macaques are not far behind. To understand the evolution of personality, health, and cognition, we need to look at more species, such as other apes, and new world monkeys.

Perhaps the greatest challenge in applying the comparative approach in individual differences research is grappling with the diverse theoretical viewpoints and approaches. The combined effect of small sample sizes, small numbers of studies, and a dearth of replications have left large gaps in the literature. In human work, replications and extensions can often be carried out by single labs because of the accessibility of experimental participants. Generating new samples for every

study is simply not feasible in primatology and animal cognition research. However, researchers in these fields could take inspiration from the similar "many labs" approach (Klein et al., 2014). The "many labs" approach brings together multiple research groups to generate reproducible and replicable results. Studies are typically pre-registered, and all participating labs contribute participants to the overall pool, lending added generalizability to the results. Labs will run the same tasks, discussed and designed in advance of data collection, and the overall results will open be apparent after the final pooled analysis, which will be more robust and powerful than results generated by traditional research. Comparative psychology's close academic cousin, developmental psychology, faces many similar data collections issues, and have taken some initial, informative steps toward addressing these issues with a many labs approach (Frank et al., 2017).

Taken together, the chapters of this thesis contribute novel empirical findings, corroborate understood associations among personality, cognition, and health, and present multiple avenues for further research. It is no longer contentious to say that animals have either personality or cognition, and these psychological capacities can be quantified meaningfully and reliably. The increasing acceptance of nonhumans' advanced psychological capacities provides an opportunity to address the interrelationships between individual differences in psychology, as well as with differences in fitness and health. Rigorous continued investigation in these areas has the potential to yield results that both illuminate the evolutionary pathways of the primate lineage and offer practical applications for psychological science.

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Appendix A: Publication list

Material included in this work has appeared in published form:

- Altschul, D. M., Terrace, H. S., & Weiss, A. (2016). Serial cognition and personality in macaques. *Animal behavior and cognition*, *3*(1), 46. **(Chapter 3).**
- Weiss, A., & Altschul, D. M. (2017). Methods and applications of animal personality research. (**Chapter 1).**
- Altschul, D. M., Wallace, E. K., Sonnweber, R., Tomonaga, M., & Weiss, A. (2017). Chimpanzee intellect: personality, performance and motivation with touchscreen tasks. *Royal Society Open Science*, *4*(5), 170169. **(Chapter 2).**

Material included in this work currently in preparation, review, or revision:

- Altschul, D.M., Morton, F.B. (2017). Guidelines for using extraction methods in data reduction analyses of social relationship structures. **(Chapter 1).**
- Altschul, D.M., Inoue-Murayama, M., Matsuzawa, T., King, J.E., Ross, S.R., Weiss, A. (2017). The personality and lifespan of chimpanzees. **(Chapter 4).**
- Altschul, D.M., Hopkins, W.D., Weiss, A. (2017). Comparing measures of allostatic load in chimpanzees and humans. **(Chapter 5).**
- Altschul, D.M., Sinn, D., Hopkins, W.D., Weiss, A. (2017). Psychological and physiological stress across cultures and species: personality's impact on allostatic load in American and Japanese humans, and chimpanzees. **(Chapter 6).**

Articles published during the period in which this thesis was written, but not featured in this document:

- Avdagic, E., Jensen, G., Altschul, D., Terrace, H. (2014). Rapid cognitive flexibility of rhesus macaques performing psychophysical task-switching. *Animal Cognition*, 17 (3), 619-631.
- Jensen, G., Altschul, D. (2015). Two perils of binary categorization: why the study of concepts can't afford true/false testing. *Frontiers in psychology*, 6.
- Wallace, E.K., Altschul, D.M., Pavonetti, S.P., Benti, B., Koerfer, K., Waller, B., Slocombe, K.S. (2017). Is music enriching for group-housed captive chimpanzees? *PLoS One*, 12 (3), e0172672.
- Robinson, L. M., Altschul, D. M., Wallace, E. K., Úbeda, Y., Llorente, M., Machanda, Z., ... & Weiss, A. (2017). Chimpanzees with positive welfare are happier, extraverted, and emotionally stable. *Applied Animal Behaviour Science*, 191, 90-97.
- Altschul, D.M., Jensen, G., Terrace, H. S. (2017). Perceptual category learning of photographic and painterly stimuli in rhesus macaques (Macaca mulatta) and humans. *PLoS One*, accepted.

Appendix B: Published supplemental materials from chapter 2

Chimpanzee Intellect: Personality, Performance, and Motivation with Touchscreen Tasks: Supplemental Materials

Drew M Altschul[1,2], Emma K Wallace[2,3], Ruth Sonnweber[4], Masaki Tomonaga[5], & Alexander Weiss[1,2]

1. The University of Edinburgh, Department of Psychology
2. Scottish Primate Research Group
3. University of York, Department of Psychology
4. University of Vienna, Department of Cognitive Biology
5. Primate Research Institute, Kyoto University

Supplemental Materials

Methods

Living Enclosure

The Royal Zoological Society of Scotland's Edinburgh Zoo Budongo Trail exhibit is a space purpose-built for chimpanzee living and research. The exhibit consists of an off-exhibit area (21.45 m^2), access tunnels (34.6 m), three indoor enclosures (125 m^2 and 14 m high), an outdoor enclosure (1,832 m^2) with a research hut attached via windows, and an multi-chamber indoor research area (26.5 m^2), referred to as the research pods [1]. The enclosure was designed to both facilitate research and allow the chimpanzees to split into multiple sub-groups, i.e. express natural fission-fusion behavior. A schematic of the enclosure is presented as Figure S1.

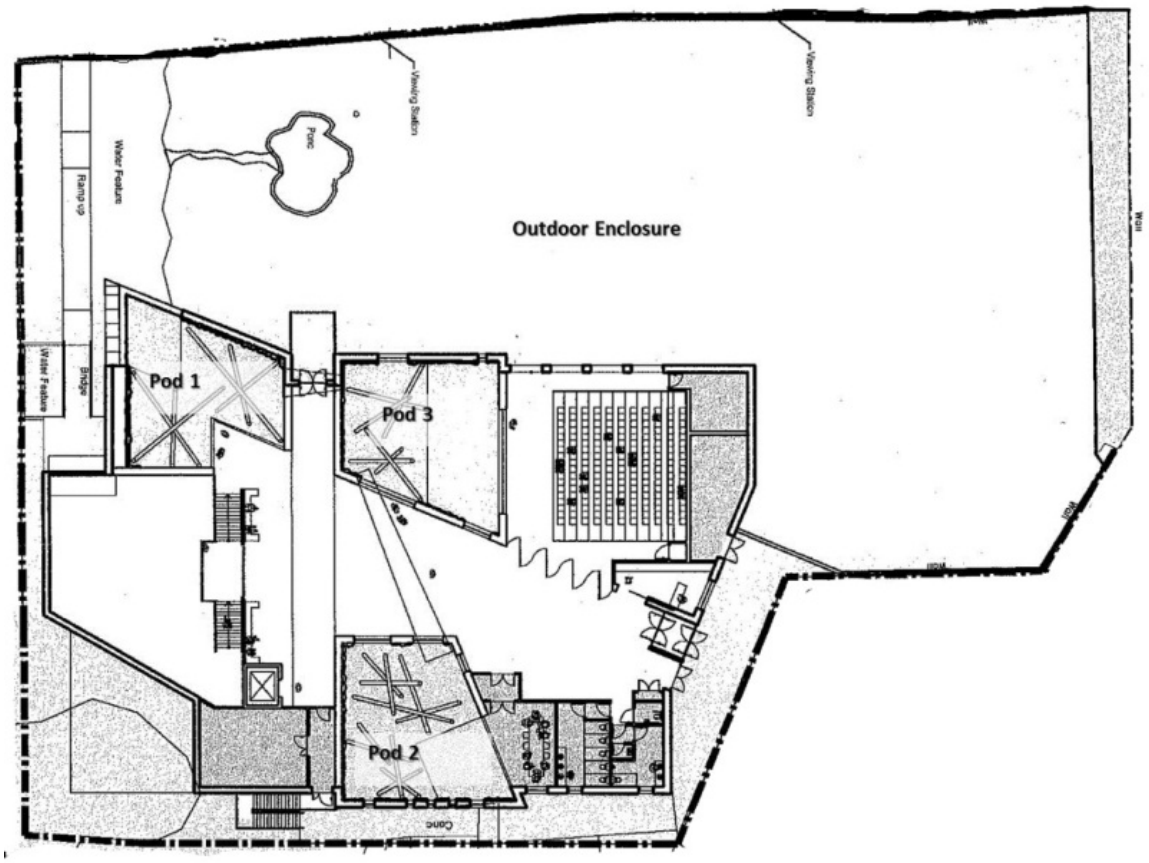

Figure S1. Layout of Budongo Trial enclosure.

Water was available ad libitum. The chimpanzees were fed via scatter feeding at least four times a day.

Participant Demographics

The study group consisted of 19 chimpanzees (eleven females, eight males; between 14 and 50 years of age). One chimpanzee died between the end of study 1 and the start of study 2. Ethical approval was obtained from the University of Edinburgh Biological Services Ethical Review Committee, and the Budongo Trail Scientific Committee.

Personality Assessment

In 2010, all chimpanzees were rated by between two and four zoo caretakers using the 54-item Hominoid Personality Questionnaire, an instrument composed of adjective items, each accompanied by two or three sentences of explanation and a 1 – 7 Likert scale [2]. Raters were instructed to rate individuals using the full spectrum of the scale, and not discuss their ratings with others. Intraclass correlations (ICCs)[3] were calculated for all items, and are showing in Table 1. Items with ICCs below zero were excluded from further analysis, and aggregate personality scores were calculated without them. In this manner, 'impulsive', 'predictable', and 'clumsy' were removed.

Table S1. Intraclass correlations of personality items

Item	ICC(3,1)	ICC(3,k)	Personality Loading[a]
Fearful	0.530	0.772	-D
Dominant	0.822	0.933	+D
Persistent	0.242	0.489	+D
Cautious	0.220	0.458	-D
Stable	0.270	0.526	-N
Autistic	0.699	0.874	+N
Curious	0.313	0.577	+O
Thoughtless	0.126	0.301	-C
Stingy	0.440	0.702	+D
Jealous	0.232	0.476	-C
Individualistic	0.031	0.087	-E
Reckless	0.464	0.722	-C
Social	0.320	0.585	+E
Distractible	0.500	0.750	-C
Timid	0.708	0.879	-D
Sympathetic	0.439	0.701	+A
Playful	0.477	0.732	+E
Solitary	0.766	0.907	-E
Vulnerable	0.350	0.618	-D

Innovative	0.566	0.797	+O
Active	0.660	0.853	+E
Helpful	0.188	0.409	+A
Bullying	0.650	0.848	+D
Aggressive	0.726	0.888	-C
Manipulative	0.392	0.659	+D
Gentle	0.623	0.832	+A
Affectionate	0.199	0.427	+E
Excitable	0.331	0.597	+N
Impulsive	-0.051	-0.172	-C
Inquisitive	0.456	0.716	+O
Submissive	0.780	0.914	-D
Cool	0.381	0.649	-N
Dependent	0.495	0.746	-D
Irritable	0.218	0.455	-C
Unperceptive	0.373	0.641	-C
Predictable	-0.011	-0.035	+C
Decisive	0.470	0.727	+D
Depressed	0.442	0.703	-E
Conventional	0.170	0.381	+A
Sensitive	0.017	0.051	+A
Defiant	0.533	0.774	-C
Intelligent	0.489	0.742	+O
Protective	0.619	0.830	+A
Quitting	0.504	0.753	-C
Inventive	0.626	0.834	+O
Clumsy	-0.012	-0.036	-C
Erratic	0.438	0.700	-C
Friendly	0.062	0.165	+E
Anxious	0.633	0.838	-D
Lazy	0.428	0.692	-E
Disorganized	0.313	0.578	-C
Unemotional	0.496	0.747	-N
Imitative	0.470	0.727	+E
Independent	0.519	0.764	+D

[a] D, Dominance; C, Conscientiousness; O, Openness; N, Neuroticism; A, Agreeableness; E, Extraversion.

Prior Experience

All chimpanzees had been habituated to the research facilities. 14 chimpanzees had received some training on a two-alternative forced choice (2AFC) task. 11 participated on a regular basis [2].

Apparatus & Access

In study 1, the apparatus consisted of a 15" touch-screen, an Apple Mac Mini, a second monitor for the experimenter, a keyboard, optical mouse, and speakers. This equipment was all mounted on a rolling table so that the apparatus could be moved around the off-exhibit areas, to where the chimpanzees could interact with it.

In study 2, the apparatus was mounted to a research window, opening onto either the indoor research pods, or the outdoor enclosure, depending on the day. In study 3, the apparatus was only used indoors. In both studies, the apparatus consisted of a 17" touchscreen monitor, a customized PC running Linux Mint, a monitor for the experimenter, a keyboard, optical mouse, speakers, and Bio-Medica Ltd. Universal Feeder [4].

All studies were participatory; the chimpanzees were free to come and go from the research areas at any time during the research sessions. When reinforcement was in place for correct trials, individuals would be given a food reward for every correct trial (e.g. half of a grape).

Experimental Programs

All programs were written in Python, and studies 2 and 3 used additional Kivy libraries. The details of the experimental approach of study 1 can be found in Sonnweber et al. [5]. Figure S2 shows the procedure for a sample trial in study 2.

Stimuli in study 1 were generated ad-hoc by the experimental program. Stimuli in study 2 were gathered in advance. Stimulus banks were sufficiently large and disparate that they could not be memorized, so all stimuli were treated as trial unique. Stimuli in study 3 did not change, as rewards were not contingent on any stimulus attributes.

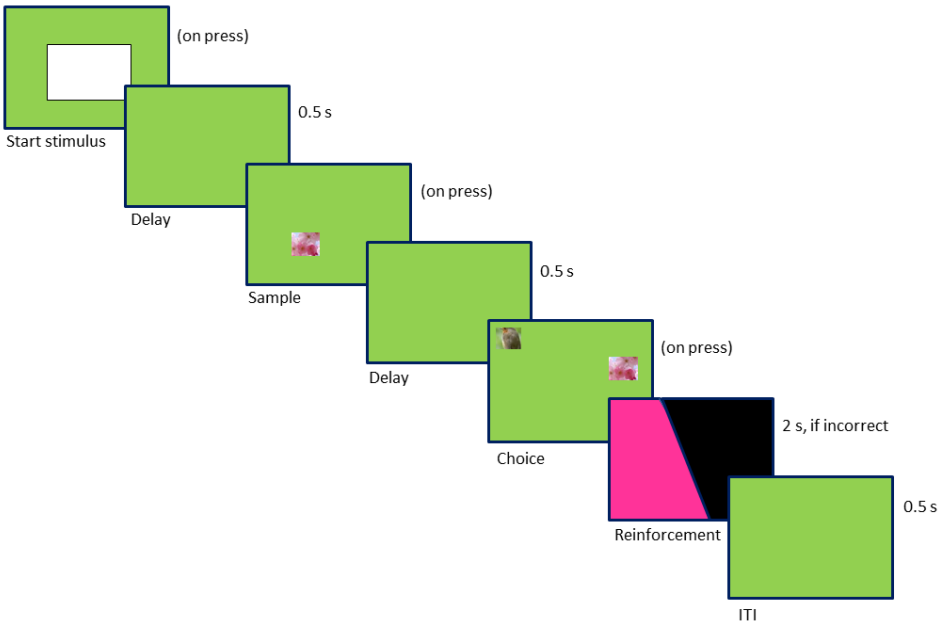

Figure S2. Procedure for task used in Study 2.

Engagement

In study 2, we collected ordinal data intended to quantify the chimpanzees' differential levels of interest in the touchscreen task, on a daily basis. No presence in the research area at any time during a research slot was coded as 0. Presence without interaction with the apparatus was coded as 1. Presence and interaction was coded as 2.

In study 3, we kept track of when individual chimpanzees progressed through different stages of training. During testing, we used audio and video recorders to keep track of when every chimpanzee entered and exited the research pods, as well as when they approached and withdrew from the touchscreen apparatus.

Results

All data analyses used standardized, centred variables, following the recommendations of Gelman [6]. To make predictors comparable in regression models, continuous variables were centred and divided by 2 standard deviations, and dichotomous variables were centred.

Study 1

Interest in participating

Two-sample Welch's *t*-tests were conducted, informed by Figure 1 (main text). Accordingly, only Dominance, Conscientiousness, Openness, and Neuroticism were tested, as the other personality dimensions showed no differences at the group level.

Drop-out

There were two training tracks for participating chimpanzees, and the two tracks had different numbers of stages during training and testing. Our data thus treated each stage for every chimpanzee as a different entry; the number of trials the chimpanzee remains at the stage was recorded, and the stage could either end with a drop-out event, or the chimpanzee continued to the next stage, in which case the entry would be censored. Gaussian frailty effects were included on an individual basis, since each individual had multiple entries, and for each distinct stage.

In addition to the Cox model, we fitted an accelerated failure time (AFT) model to these data, as Cox and AFT models are comparable, but have different advantages. The model specification was the same, except that due to technical limitations, frailty effects were only included for the individual. Based on likelihood-ratio tests, the Weibull distribution was the best distribution for the AFT model given these data. Compared to the Cox model, however, the AFT model did not improve fit (likelihood-ratio test; χ = -76.2, df = 0.06, $p \approx 1$). Nevertheless, the results of both models were not substantively different, and while power could not be calculated for the AFT model, the power to detect the significant effects of Conscientiousness and Agreeableness in the Cox model were 93% and 95%, respectively. The AFT model is described in Table S2.

Table S2. AFT model of drop-out from study 1

Parameter	*β*	95%	C.I.
Dominance	-1.05	[-3.77,	1.67]
Conscientiousness	**2.96**	**[1.04,**	**4.87]**
Openness	1.08	[-0.55,	2.71]
Neuroticism	-1.29	[-4.35,	1.78]
Agreeableness	**-2.45**	**[-3.69,**	**-1.20]**
Extraversion	1.07	[-0.29,	2.42]
scale	0.546		

Learning Speed

Learning speed was quantified in two ways. First, we fitted another Cox model, using the same number of trial data from our earlier drop-out model, but if an individual reached criterion after that many trials they were assigned a completion event, otherwise they were censored. The completion event list is not the inverse of the above drop-out event list, as there are quite a few entries where an individual did not meet criterion, but did not drop out, either. In these cases, the individual was shifted to a different task, which was not more advanced than the previous task. The results of this model are shown in Table S3. No personality dimensions were associated with survival time and completion of different stages.

Second, we excluded stages where the chimpanzee did not reach criterion, and fitted a Poisson GLMM to the number of trials it took an individual to reach criterion at a given stage. We again included random effects for individual and stage. The results of this model are shown in Table S3.

Table S3. Models of learning speed from study 1

	Cox model of completed stages			Poisson model of trials to criterion		
Parameter	*β*	95%	C.I.	*β*	95%	C.I.
Dominance	-0.21	[-1.78,	1.36]	0.74	[-0.29,	1.76]
Conscientiousness	-0.13	[-1.20,	0.94]	**0.88**	**[0.03,**	**1.74]**
Openness	0.02	[-1.43,	1.47]	0.96	[-0.66,	0.85]
Neuroticism	0.29	[-1.48,	2.07]	-0.15	[-1.44,	1.14]
Agreeableness	0.49	[-0.62,	1.59]	-0.57	[-1.22,	0.08]
Extraversion	-0.28	[-1.41,	0.85]	-0.29	[-0.97,	0.39]

The significant effect of Conscientiousness on number of trials to reach criterion is likely due to the bias of high Conscientiousness individuals staying in the study for longer. Individuals who remained in the study were exposed to more and more difficult stages of the task, which would take more and more trials to complete. The power to detect the effect of Conscientiousness in this Cox model was 73%

Accuracy

We included all training and testing trials in our analyses of accuracy. Across all GLMMs we included random effects of participant, stage, and trial type (training or probe, *cf.* Sonnweber at al. [5]).

Our initial model included only personality, predicting correctness of response as a binomial outcome (Table S4). We also wished to establish

whether or not there were training effects, so we updated our model by adding date as an additional covariate. Including date significantly improved model fit (likelihood-ratio test; $\chi^2 = 56.4$, df = 1, $p < 0.0001$). To test for within-session effects, we added the trial number to the model, but this did not improve fit (likelihood-ratio test; $\chi^2 = 0.042$, df = 1, $p \approx 0.84$). This left the model which included personality and date as the best fit for the data (Table 1, main text).

Table S4. Initial GLMM of accuracy in study 1

Parameter	*β*	95%	CI
Dominance	**-0.25**	**[-0.51,**	**0.00]**
Conscientiousness	**0.28**	**[0.04,**	**0.53]**
Openness	0.11	[-0.15,	0.37]
Neuroticism	-0.04	[-0.37,	0.28]
Agreeableness	-0.18	[-0.38,	0.03]
Extraversion	**0.27**	**[0.07,**	**0.46]**

The power to detect the effects of Dominance, Conscientiousness, and Extraversion was calculated for these three models of accuracy. In the initial model (Table S4), power was 81%, 93%, and 96%, respectively. In the model in including date (Table 1), power was 63%, 65%, and 88%, respectively. In the model including date and trial (Table S4), power was 59%, 67%, and 83%, respectively.

Response Time

The outcome variable, response time (RT), was log transformed for use in all regressions. We fit two sets of models: the first modelled all RT data, the second modelled only RT data from trials where the participant responded correctly, i.e. error free trials. Our models of the latter data were used in our interpretations of RT, though they did not markedly differ from the models which included all trials.

Our initial model of all log transformed RTs only included personality (Table S5). Including date did not improve the model fit (likelihood-ratio test; $\chi^2 = 3.0$, df = 1, $p \approx 0.08$). Our initial model of the log transformed RTs from correct responses again included only personality (Table S5), and again, adding date did not significantly improve the fit of the model (likelihood-ratio test; $\chi^2 = 0.2$, df = 1, $p \approx 0.65$).

Table S5. Log-gamma GLMMs of RT data in study 1

	All trials			Correct trials		
Parameter	*β*	95%	CI	*β*	95%	CI
Dominance	0.14	[-0.46,	0.74]	0.10	[-0.42,	0.61]
Conscientiousness	**-0.61**	**[-1.05,**	**-0.16]**	**-0.53**	**[-0.92,**	**-0.14]**
Openness	**-0.51**	**[-0.94,**	**-0.08]**	**-0.38**	**[-0.76,**	**-0.01]**
Neuroticism	0.09	[-0.63,	0.82]	-0.03	[-0.69,	0.62]
Agreeableness	0.40	[-0.06,	0.75]	0.27	[-0.05,	0.60]
Extraversion	**-0.47**	**[-0.79,**	**-0.15]**	**-0.39**	**[-0.67,**	**-0.10]**

Touch patterns

The experimental task recorded the number of touches an individual made to the screen on every trial. While some individuals were quite precise, some were sloppier than others and sometimes simple errors occurred.

We fit GLMMs using a Poisson link function, as the data were counts. Our initial model included only personality variables. Including date as a covariate did not significantly improve model fit (likelihood-ratio test; $\chi^2 = 3.6$, df = 1, $p \approx 0.06$), so our final and initial models were the same (Table S7). High Conscientiousness chimpanzees tended to make fewer touches to the screen on any given trial. The power to detect this effect was 77%.

Table S6. Poisson model of number of touches, per trial

Parameter	*β*	95%	CI
Dominance	-0.09	[-0.54,	0.34]
Conscientiousness	**-0.38**	**[-0.76,**	**-0.00]**
Openness	-0.15	[-0.49,	0.19]
Neuroticism	-0.01	[-0.57,	0.54]
Agreeableness	0.13	[-0.16,	0.42]
Extraversion	-0.09	[-0.39,	0.21]

Study 2

Engagement

Engagement data were based on 20 days when testing occurred in the outdoor research area, and 28 days which took place in the indoor research pods. Engagement data was collected for every individual, for every day of testing. An individual was assigned to one of three escalating levels: 0 – the individual did not enter the research area or did not show any interest in the

touchscreen, 1 – the individual showed interest in and approached the touchscreen, but did not complete any trials, and 2 – the individual interacted with the touchscreen and completed as least one trial.

While the individuals who never participated and showed no interest tended not to waver in this behavior, most individuals who showed interest and approached the screen but did not complete a trial did at some point participate in multiple trials of the task. In order to visualize trends in chimpanzees' behavior across all sessions, we plotted all six personality dimensions, split into three groups: those who never participated, those who completed multiple trials, and those that completed entire sessions (Figure S3).

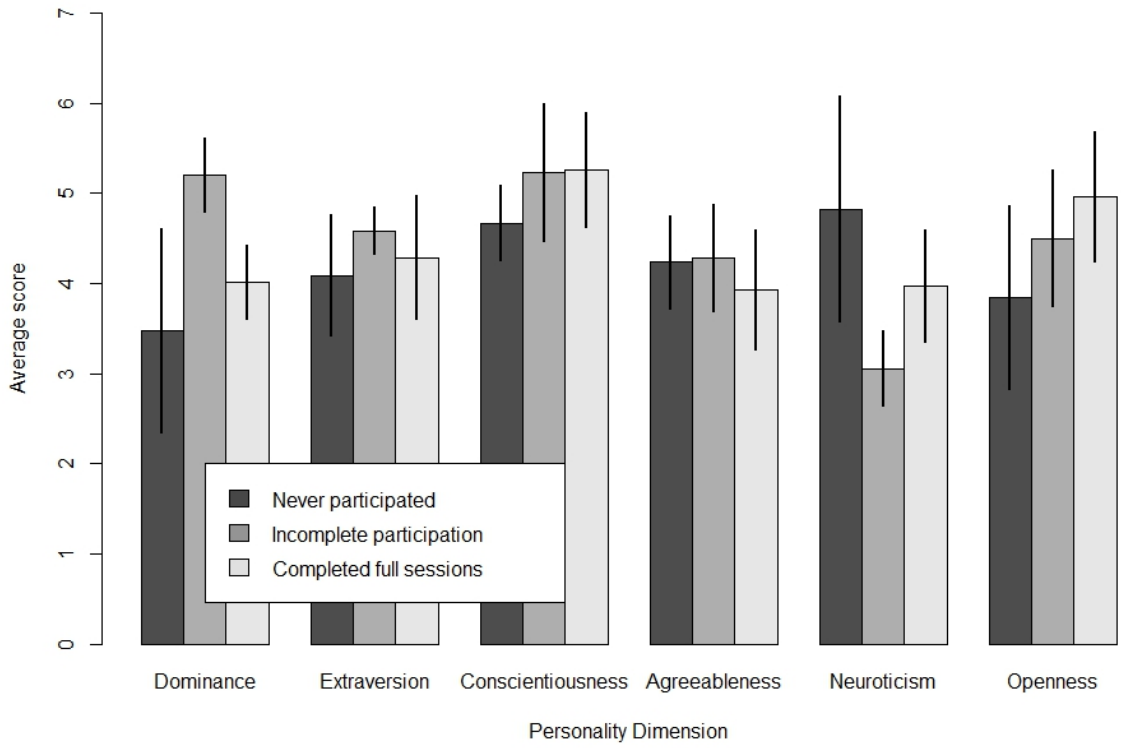

Figure S3. Personality of chimpanzees, split by level of participation in Study 2.

Note. Error bars represent standard errors around the mean.

To account for the ordered categorical nature of the engagement data, we fit cumulative link mixed models (CLMM) to assess how personality predicted participation. In all models, participant was included as a random effect, and location (indoor or outdoor research area) was included as a fixed effect for technical reasons.

Our base model included only personality and location as predictors. Because of what appeared to be non-linear relationships between participation and both Dominance and Neuroticism (Figure S3), we added quadratic effects for both predictors. Neither quadratic Dominance (likelihood-ratio test; $\chi^2 = 1.4$, df = 1, $p \approx 0.24$), nor quadratic Neuroticism (likelihood-ratio test; $\chi^2 = 0.2$, df = 1, $p \approx 0.65$) improved fit, so the final model only included linear personality predictors (Table 2, main text).

Accuracy

Performance analyses were based on a total of 1870 trials from 14 chimpanzees. As in study 1, our first model included only personality predictors, and we fit a second model which included date as an additional covariate, to probe for training effects. Including date did not significantly improve the fit of the model (likelihood-ratio test; $\chi^2 = 1.6$, df = 1, $p \approx 0.20$). Our initial and final models were thus the same (Table 2, main text). The power to detect the effect of Openness in this model was 50%.

Response Time

Two RT periods were available for analysis: the time between presentation of the sample screen and response, and the time between presentation of the test screen and response. We labelled the first of these "processing time" (PT) and the second "inspection time" (IT). PT and IT were both log-transformed before being regressed.

As in previous models, we entered date as an additional predictor and evaluated its effect on fit, and found a significant improvement (likelihood-ratio tests; PT: $\chi^2 = 287.6$, df = 1, $p < 0.0001$; IT: $\chi^2 = 127.8$, df = 1, $p < 0.0001$). We then entered trial to the model, which also significantly improved the IT model ($\chi^2 = 40.0$, df = 1, $p < 0.0001$), but the PT model wold not converge when trial was included, so we settled on the PT model including date as our final model. In the final models (Table S7), date and trial showed significant, negative associations with RT measures, indicating that within and across training days, RTs became faster over time. We also found a significant relationship between Extraversion and both PT (power: 88%) and IT (power: 97%), indicating that higher Extraversion individuals responded faster.

Table S7. RT models from study 2

	Processing Time			Inspection Time		
Parameter	*β*	95%	CI	*β*	95%	CI
Dominance	0.44	[-0.34,	1.10]	0.38	[-0.02,	0.77]
Conscientiousness	-0.20	[-0.72,	0.52]	-0.14	[-0.44,	0.15]
Openness	-0.22	[-0.74,	0.13]	-0.14	[-0.43,	0.15]
Neuroticism	-0.49	[-1.52,	0.53]	-0.41	[-0.91,	0.09]
Agreeableness	0.02	[-0.47,	0.51]	0.03	[-0.23,	0.30]
Extraversion	**-0.54**	**[-0.98,**	**-0.10]**	**-0.36**	**[-0.60,**	**-0.13]**
Date	-0.42	[-0.47,	-0.37]	-0.42	[-0.48,	-0.37]
Trial				-0.18	[-0.22,	-0.14]

We also analysed PT and IT including only correct trials. The models featuring date and trial were the best fit (PT: χ^2 = 133.8, df = 2, p < 0.0001; IT: 167.8, df = 2, p < 0.0001). The final models are shown in Table S8; the models differed from those which analysed all trials: faster PT was associated with lower Dominance, and higher Extraversion (power: 95%, 84%), while faster IT was associated with lower Dominance, and higher Extraversion, Agreeableness, and Neuroticism (power: 77%, 86%, 26%, 77%). Date and trial continued to have similar effects. As in study 1, we used the final models of the correct trials for interpretation.

Table S8. RT models of correct responses from study 2

	Processing Time			Inspection Time		
Parameter	*β*	95%	CI	*β*	95%	CI
Dominance	**0.54**	**[0.07,**	**1.01]**	**0.49**	**[0.24,**	**0.74]**
Conscientiousness	-0.13	[-0.47,	0.20]	-0.01	[-0.22,	0.19]
Openness	-0.18	[-0.16,	0.53]	-0.11	[-0.10,	0.31]
Neuroticism	-0.49	[-1.09,	0.09]	**-0.49**	**[-0.77,**	**-0.20]**
Agreeableness	-0.03	[-0.34,	0.28]	**-0.25**	**[-0.44,**	**-0.06]**
Extraversion	**-0.34**	**[-0.63,**	**-0.05]**	**-0.39**	**[-0.55,**	**-0.23]**
Date	-0.38	[-0.45,	-0.30]	-0.39	[-0.47,	-0.32]
Trial	-0.12	[-0.18,	-0.06]	-0.18	[-0.24,	-0.13]

Study 3

Progression of training

The first four phases presented combinations of horizontal buttons. The buttons were randomly placed on the screen, and each was associated with a

category of sound: pop music, classical music, or silence. The buttons are shown in representative presentations in Figure S4.

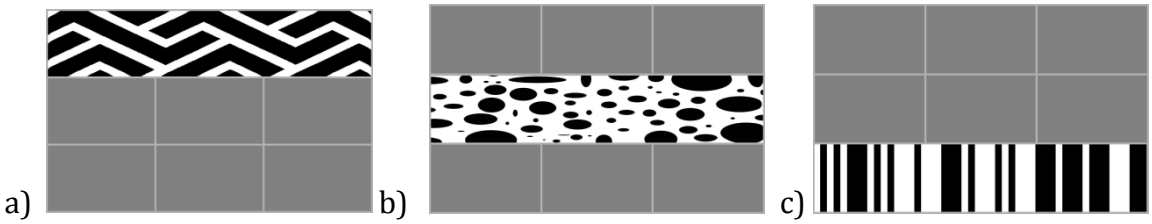

Figure S4. Images of the three touchscreen buttons, as they appeared during phases 1 - 4. When pressed, each initiated the following actions: (a) turned on classical music for three seconds, (b) turned music off / continued silence for three seconds and (c) turned on pop music for three seconds.

After pressing a button and receiving a reward 10 times, an individual would progress to the next phase. If an individual did not complete a phase within a single approach to the touchscreen, then the remaining button presses were completed the next time the individual approached the touchscreen, whether it was later in the session or on another day.

In phase 5, the task changed slightly, and is visually described in Figure S5.

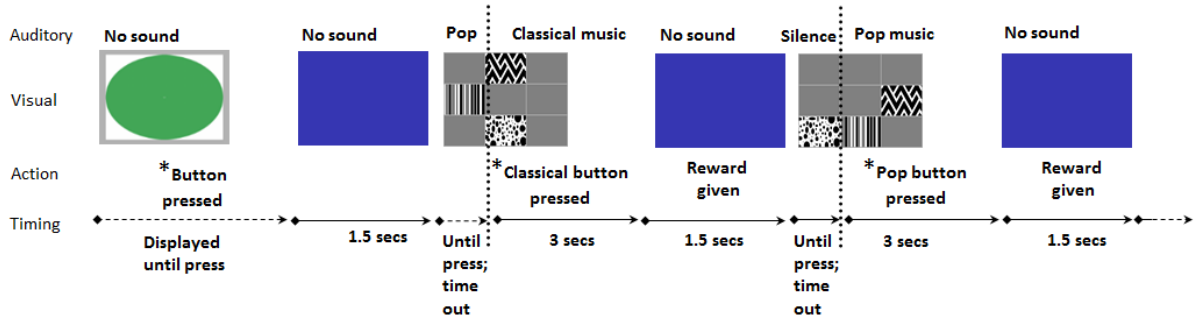

Figure S5. Example first two trials during a session of phase 5, progressing from left to right. Phase 5 continued until 40 buttons, not including the green start button, had been successfully pressed. If the touchscreen was not interacted with for 30 seconds, it reverted back to the green circle screen.

Individuals had to complete 40 trials; 10 where the appearance of the buttons on the screen coincided with classical music playing at onset of the grid screen, 10 in which buttons appeared with pop music playing, and 20 where no music accompanied the appearance of the grid screen. The order of these trials was randomised. Again, if an individual did not complete the testing within a single approach of the touchscreen or experimental session then the remaining button presses were completed the next time the individual approached the touchscreen, whether it was later in the session or on another day.

In phase 6, rewards were no longer given out for pressing buttons on the touchscreen. To encourage the chimpanzees to enter the research pods, a bale of straw (approximately 10kg) and 7kg of primate pellets were spread across the two pods. As the chimpanzees were let into the research pods the touchscreen displayed the three buttons in a randomised positions on the 3x3 grid. For three sessions classical music was already playing as the individuals entered the pods, for three sessions pop music was playing, for three sessions there was silence, and for three sessions the touchscreen was not physically available to the participants and no music played (total of 12 sessions). The sound would continue until a button was pressed or the trial ended after 60 minutes. If an individual approached the touchscreen and pressed a button, the corresponding genre of music would play or the music would be turned off until a new button was pressed. If the touchscreen was silent and the silence button was pressed then silence would continue. If music was playing and the same music button was pressed, a different randomly selected piece of music from the same category would begin playing. If no new button was pressed that music or silence would continue until the end of the trial. Otherwise, the task procedure was the same as in Figure S5. Data was collected on how long individuals were present in the pod, how many approaches were made to the screen, and how long individuals spent in front of the screen.

Differences in trained vs. untrained groups

As in study 1, chimpanzees were split into two groups, participants and non-participants, and personality was plotted having been divided along these lines (Figure S6).

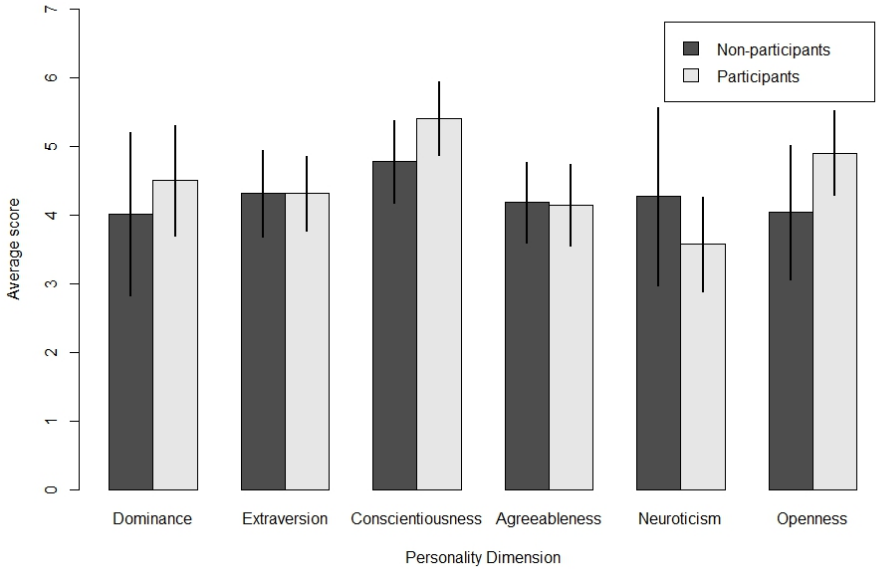

Figure S6. Personality of chimpanzees, split by level of participation in Study 3. Error bars represent standard errors around the mean.

Time spent in the research pods

The time data were inflated with zeroes as some chimpanzees never entered the pods on certain days. Zero-inflation is difficult to model with GLMMs, though the presence of zeroes does not necessarily mean that the assumption of the Poisson model are violated [7].

Thus, we first fit a Poisson GLMM to the model, and tested for overdispersion. This model was overdispersed (χ^2 = 2827, df = 207, $p < 0.0001$), so we modelled these data using a negative binomial (NB) GLMM, which is often better suited for overdispersed data [8]. Moreover, the NB model fit the data better than the Poisson model (AIC_{NB} = 1519.4, $AIC_{Poisson}$ = 3782.8), so we interpreted the output of the NB model (Table S9). The power to detect the effect of Extraversion in this model was 81%.

Table S9. NB model of time spent in research pods

Parameter	*β*	95% CI	
Dominance	-0.14	[-1.60,	1.31]
Conscientiousness	-0.25	[-1.13,	0.63]
Openness	-0.06	[-0.79,	0.66]
Neuroticism	-0.61	[-2.08,	0.85]
Agreeableness	-0.28	[-0.96,	0.42]
Extraversion	**0.78**	**[0.06,**	**1.51]**

Approaches to the screen

As the data included one line per chimpanzee, and some chimpanzees never approached the screen, the data had the potential to be zero-inflated. We first fit a Poisson model and tested for overdispersion, and concluded that the Poisson model was overdispersed (z = 2.71, $p < 0.005$). We again fell back on a NB model (Table S10), which fit the data better than the Poisson model (AIC_{NB} = 91.89, $AIC_{Poisson}$ = 108.0).

Table S10. NB model of number of approaches to screen

Parameter	*β*	95% CI	
Dominance	-0.19	[-1.67,	1.15]
Conscientiousness	**1.09**	**[0.15,**	**2.16]**
Openness	0.46	[-0.43,	1.46]
Neuroticism	0.10	[-1.43,	1.48]
Agreeableness	**-0.93**	**[-1.63,**	**-0.28]**
Extraversion	0.69	[-0.19,	1.70]

Time spent at the screen

Every time a chimpanzee approached the experimental apparatus, we timed how long the individual spent in front of and interacting with the touchscreen. Since the time spent at the screen was always at least a second, there were no zeroes in the data, and no need to accommodate inflation. 1 outlier greater than 3 standard deviations from the mean was removed. A Poisson GLMM was fit with personality covariates (Table S11). The power to detect the effects of Openness and Extraversion was 96% and 87%.

Table S11. Poisson model of time spent at screen

Parameter	*β*	95% CI	
Dominance	0.26	[-0.20,	0.73]
Conscientiousness	0.21	[-0.17,	0.59]
Openness	**0.52**	**[0.21,**	**0.83]**
Neuroticism	0.41	[-0.10,	0.91]
Agreeableness	0.19	[-0.04,	0.43]
Extraversion	**-0.36**	**[-0.66,**	**-0.05]**

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Appendix C: The 54-item Hominoid Personality Questionnaire

CHIMPANZEE PERSONALITY TRAIT ASSESSMENT

Chimpanzee personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits listed on the following pages. Make your judgments on the basis of your own understanding of the trait guided by the short clarifying definition following each trait. The chimpanzee's own behaviors and interactions with other chimpanzees should be the basis for your numerical ratings. Use your own subjective judgment of typical chimpanzee behavior to decide if the chimpanzee you are scoring is above, below, or average for a trait. The following seven point scale should be used to make your ratings.

1. **Displays either total absence or negligible amounts of the trait.**
2. **Displays small amounts of the trait on infrequent occasions.**
3. **Displays somewhat less than average amounts of the trait.**
4. **Displays about average amounts of the trait.**
5. **Displays somewhat greater than average amounts of the trait.**
6. **Displays considerable amounts of the trait on frequent occasions.**
7. **Displays extremely large amounts of the trait.**

Please give a rating for each trait even if your judgment seems to be based on a purely subjective impression of the chimpanzee and you are somewhat unsure about it. Indicate your rating by placing a cross in the box underneath the chosen number. $\boxed{\times}$

Finally, do not discuss your rating of any particular chimpanzee with anyone else. As explained in the handout accompanying this questionnaire, this restriction is necessary in order to obtain valid reliability coefficients for the traits.

CHIMPANZEE PERSONALITY TRAIT ASSESSMENT

Chimpanzee's full name:_____

Rater's full name:_____

Date (Mon/Day/Yr):_____

FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

DOMINANT: Subject is able to displace, threaten, or take food from other chimpanzees. Or subject may express high status by decisively intervening in social interactions.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

PERSISTENT: Subject tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from other chimpanzees.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

CAUTIOUS: Subject often seems attentive to possible harm or danger from its actions. Subject avoids risky behaviors.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

STABLE: Subject reacts to its environment including the behavior of other chimpanzees in a calm, equable, way. Subject is not easily upset by the behaviors of other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

AUTISTIC: Subject often displays repeated, continuous, and stereotyped behaviors such as rocking or self clasping.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

CURIOUS: Subject has a desire to see or know about objects, devices, or other chimpanzees. This includes a desire to know about the affairs of other chimpanzees that do not directly concern the subject.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

THOUGHTLESS: Subject often behaves in a way that seems imprudent or forgetful.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

STINGY/GREEDY: Subject is excessively desirous or covetous of food, favored locations, or other resources in the enclosure. Subject is unwilling to share these resources with others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

JEALOUS: Subject is often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social groups. Subject may attempt to disrupt activities of advantaged chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INDIVIDUALISTIC: Subject's behavior stands out compared to that of the other individuals in the group. This does not mean that it does not fit or is incompatible with the group.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

RECKLESS: Subject is rash or unconcerned about the consequences of its behaviors.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SOCIABLE: Subject seeks and enjoys the company of other chimpanzees and engages in amicable, affable, interactions with them.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DISTRACTIBLE: Subject is easily distracted and has a short attention span.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

TIMID: Subject lacks self confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SYMPATHETIC: Subject seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

PLAYFUL: Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviors with or without other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SOLITARY: Subject prefers to spend considerable time alone not seeking or avoiding contact with other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

VULNERABLE: Subject is prone to be physically or emotionally hurt as a result of dominance displays, highly assertive behavior, aggression, or attack by another chimpanzee.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INNOVATIVE: Subject engages in new or different behaviors that may involve the use of objects or materials or ways of interacting with others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

ACTIVE: Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

HELPFUL: Subject is willing to assist, accommodate, or cooperate with other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

BULLYING: Subject is overbearing and intimidating towards younger or lower ranking chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

AGGRESSIVE: Subject often initiates fights or other menacing and agonistic encounters with other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

MANIPULATIVE: Subject is adept at forming social relationships for its own advantage, especially using alliances and friendships to increase its social standing. Chimpanzee seems able and willing to use others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

GENTLE: Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

AFFECTIONATE: Subject seems to have a warm attachment or closeness with other chimpanzees. This may entail frequently grooming, touching, embracing, or lying next to others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

EXCITABLE: Subject is easily aroused to an emotional state. Subject becomes highly aroused by situations that would cause less arousal in most chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

IMPULSIVE: Subject often displays some spontaneous or sudden behavior that could not have been anticipated. There often seems to be some emotional reason behind the sudden behavior.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INQUISITIVE: Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about other chimpanzees, objects, or persons within its view.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SUBMISSIVE: Subject often gives in or yields to another chimpanzee. Subject acts as if it is subordinate or of lower rank than other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

COOL: Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DEPENDENT/FOLLOWER: Subject often relies on other chimpanzees for leadership, reassurance, touching, embracing and other forms of social support.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

IRRITABLE: Subject often seems in a bad mood or is impatient and easily provoked to anger exasperation and consequent agonistic behavior.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

UNPERCEPTIVE: Subject is slow to respond or understand moods, dispositions, or behaviors of others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

PREDICTABLE: Subject's behavior is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual behavioral routine.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DECISIVE: Subject is deliberate, determined, and purposeful in its activities.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DEPRESSED: Subject does not seek out social interactions with others and often fails to respond to social interactions of other chimpanzees. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

CONVENTIONAL: Subject seems to lack spontaneity or originality. Subject behaves in a consistent manner from day to day and stays well within the social rules of the group.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SENSITIVE: Subject is able to understand or read the mood, disposition, feelings, or intentions of other chimpanzees often on the basis of subtle, minimal cues.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DEFIANT: Subject is assertive or contentious in a way inconsistent with the usual dominance order. Subject maintains these actions despite unfavorable consequences or threats from others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INTELLIGENT: Subject is quick and accurate in judging and comprehending both social and non-social situations. Subject is perceptive and discerning about social relationships.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

PROTECTIVE: Subject shows concern for other chimpanzees and often intervenes to prevent harm or annoyance from coming to them.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

QUITTING: Subject readily stops or gives up activities that have recently been started.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INVENTIVE: Subject is more likely than others to do new things including novel social or non-social behaviors. Novel behavior may also include new ways of using devices or materials.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

CLUMSY: Subject is relatively awkward or uncoordinated during movements including but not limited to walking, acrobatics, and play.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

ERRATIC: Subject is inconsistent, indefinite, and widely varying in its behavior and moods.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

FRIENDLY: Subject often seeks out contact with other chimpanzees for amiable, genial activities. Subject infrequently initiates hostile behaviors towards other chimpanzees.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

ANXIOUS: Subject often seems distressed, troubled, or is in a state of uncertainty.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

LAZY: Subject is relatively inactive, indolent, or slow moving and avoids energetic activities.

least						most
1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

DISORGANIZED: Subject is scatterbrained, sloppy, or haphazard in its behavior as if not following a consistent goal.

least						most
1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

UNEMOTIONAL: Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.

least						most
1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

IMITATIVE: Subject often mimics, or copies behaviors that it has observed in other chimpanzees.

least						most
1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

INDEPENDENT: Subject is individualistic and determines its own course of action without control or interference from other chimpanzees.

least						most
1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐
