

Review Paper

Cite this article: Lages YV and McNaughton N. (2022) Non-human contributions to personality neuroscience – from fish through primates. An introduction to the special issue. *Personality Neuroscience*. Vol 5: e11, 1–9. doi: [10.1017/pen.2022.4](https://doi.org/10.1017/pen.2022.4)

Received: 28 July 2022
Revised: 18 August 2022
Accepted: 24 August 2022



Keywords:

Evolution; Personality; Psychopathology; Neuroscience; Translation

Author for correspondence:

Neil McNaughton,
Email: neil.mcnaughton@otago.ac.nz

Non-human contributions to personality neuroscience – from fish through primates. An introduction to the special issue

Yury V. Lages¹  and Neil McNaughton² 

¹Department of Psychology, Pontifical Catholic University of Rio de Janeiro, Rio de Janeiro, Brazil and ²Department of Psychology, University of Otago, Dunedin, New Zealand

Abstract

The most fundamental emotional systems that show trait control are evolutionarily old and extensively conserved. Psychology in general has benefited from non-human neuroscience and from the analytical simplicity of behaviour in those with simpler nervous systems. It has been argued that integration between personality, psychopathology, and neuroscience is particularly promising if we are to understand the neurobiology of human experience. Here, we provide some general arguments for a non-human approach being at least as productive in relation to personality, psychopathology, and their interface. Some early personality theories were directly linked to psychopathology (e.g., Eysenck, Panksepp, and Cloninger). They shared a common interest in brain systems that naturally led to the use of non-human data; behavioural, neural, and pharmacological. In Eysenck's case, this also led to the selective breeding, at the Maudsley Institute, of emotionally reactive and non-reactive strains of rat as models of trait neuroticism or trait emotionality. Dimensional personality research and categorical approaches to clinical disorder then drifted apart from each other, from neuropsychology, and from non-human data. Recently, the conceptualizations of both healthy personality and psychopathology have moved towards a common hierarchical trait perspective. Indeed, the proposed two sets of trait dimensions appear similar and may even be eventually the same. We provide, here, an introduction to this special issue of *Personality Neuroscience*, where the authors provide overviews of detailed areas where non-human data inform human personality and its psychopathology or provide explicit models for translation to human neuroscience. Once all the papers in the issue have appeared, we will also provide a concluding summary of them.

This paper provides background for focussed reviews that will make up a Special Issue, *Non-human contributions to personality neuroscience – from fish through primates*. It also invites pre-submission enquiries.¹

The Special Issue aims to make clear: (1) that non-human work of all types allows comparative analysis (from fish through primates) important for theories of personality in general and personality neuroscience in particular; (2) how strain derivation and neural manipulations generate non-human results that inform traits, particularly those of interest in human psychopathology (where Eysenck's 3-factor model is still held in high regard, albeit with a need to rename his factors); (3) that observational non-human work, particularly in primates, can link to and inform the Big 5, HEXACO, etc; (4) that the different forms of non-human work can be naturally linked through study of the conserved brain systems involved – and so provide a basis for the integration of current hierarchical trait models of psychopathology (e.g., MMPI and HiTOP) with hierarchical trait models of healthy personality; (5) that, particularly between species, neural variation can help us link personality to brain systems. In sum, the Special Issue aims to show that, because of phylogenetic conservation of fundamental traits, even organisms as simple as fish can provide an architectural bedrock on which we can progressively build our understanding of the more elaborate superstructures on which personality depends in more complex organisms.

We believe that direct contact with neurobiology, both for derivation of measures and their validation (see Section 6), is crucial for more mechanistic, explanatory, theory in personality research. “Personality is an abstraction used to explain consistency and coherency in an individual's pattern of affects, cognitions, desires and behaviors. . . . The task of the personality researcher is to identify the consistencies and differences within and between individuals . . . and . . . to explain them” (Revelle, 2007, p. 37, our emphasis). Where the explanation is neural, all current theories must align with a single set of known neuropsychological facts – with the brain (and phylogenetically conserved functions) providing a Rosetta stone to translate between

© The Author(s), 2022. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

the theoretical systems. Neurobiology should help us unite the Big-5, HiTOP, and Eysenck/Gray/RST approaches. Since these approaches originate in different top-down and bottom-up perspectives, integrating them across all the different motivational brain networks and levels of explanation should hit home in the heartlands of mainstream personality psychology. But first, we provide some background to this approach.

1. Darwin and the conservation of emotions

“On the Origin of Species by Means of Natural Selection” (Darwin, 1859) focused on non-human animals and plants to reduce opposition. It, nonetheless, implied that humans had been subject to natural selection. Ten years later, “The Descent of Man” and “Expression of the emotions in man and animals” (Darwin, 1871, 1872) treated humans as just another animal – with evolved, often phylogenetically conserved, emotions as well as morphology.

Based on his observation of facial expressions in humans, Darwin identified a few core emotions (e.g., happiness, sadness, fear, and surprise) that would have common features across cultures (Snyder, Kaufman, Harrison, & Maruff, 2010) and be based on emotional systems that are evolutionarily old and largely conserved. The importance of facial expressions for social communication in primates (Altschul, Robinson, Coleman, Capitanio, & Wilson, 2019; Wilson et al., 2020) is consistent with Darwin’s original hypothesis.

“Emotion” clearly encompasses states of affect, behaviour, cognition, and desire that sustain life using fundamental “survival circuits” (Ekman, 1992; Ledoux, 2012). However, “What is an emotion?” (James, 1884) is still answered in different ways by different people, and we have argued (McNaughton, 1989) that an emotion is most easily characterized by the “goals” (“teleonomy”, Pittendrigh, 1958) of its phylogenetic history.

If a change in state is adaptive, trait sensitivity must also depend on adaptive value (Blanchard & Blanchard, 1989). The long-term trait control of emotions and its linkage to neurological and psychiatric illness (Greene et al., 2020; McNaughton, 2020) make non-human models of emotional behaviour a valuable platform to study the conserved fundamental states and traits contributing to human emotions. According to Darwin, comparative work is less “liable to confound conventional or artificial gestures and expressions with those which are innate or universal” (Darwin, 1872, p. 50).

2. Conservation of brain systems

If trait patterns of emotion-related behaviour are conserved, so must be their brain mechanisms, which will be central to understanding the neural basis of personality. Subcortical structures are the primary responders to, and organisers of, responses to emotionally relevant stimuli (Barrett, 2017; Ledoux, 1991, 1996; Lopes da Silva, Witter, Boeijinga, & Lohman, 1990; MacLean, 1949, 1952). Thus, the subcortex is where we must first look for the long-term sensitivities that underlie personality; it is also important for cognition (Janacek et al., 2022).

The periaqueductal grey (PAG) is the lowest level of the *integrated* control of emotions and has highly conserved structure and gene and protein expression across vertebrates (O’Connell & Hofmann, 2012). The PAG, hypothalamus, and amygdala are inter-connected in ancient systems that provide the most basic organised control of responses directed to appetitive and aversive goals, and to conflicts between appetite and aversion – with each of

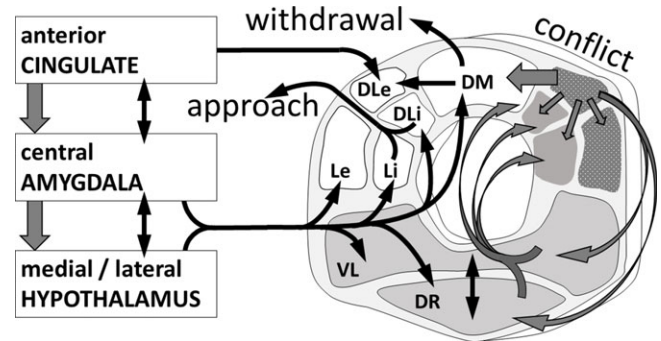


Figure 1. The organization of goal control within the PAG/DR and in relation to hierarchically organized afferents. From Silva and McNaughton (2019) with permission.

these 3 types of process controlled by a different part of the PAG (Figure 1). Posterior/dorsal PAG organises basic aversion, anterior/lateral PAG organises appetite and courtship (Comoli, Ribeiro-Barbosa, & Canteras, 2003; Kyuhou & Gemba, 1998; Mota-Ortiz, Sukikara, Felicio, & Canteras, 2009); and dorsolateral PAG and dorsal raphe organise responses to conflict between positive and negative goals (Figure 1). Separate PAG areas control active versus passive coping strategies (Keay & Bandler, 2015).

From PAG, through hypothalamus, to amygdala, neural control is well conserved relative to basal vertebrates. The PAG also receives descending input from the habenula, which is essentially unchanged from the lamprey through vertebrates (Loonen & Ivanova, 2015, 2016), despite involvement in many higher order processes (Hones & Mizumori, 2022; Loonen & Ivanova, 2019; Rolls, 2017). Further, “the habenula . . . plays an essential role in regulating the intensity of reward-seeking and adversity-avoiding behavior . . . by regulating the activity of ascending midbrain monoaminergic tracts” (Loonen & Ivanova, 2019, p. 233), which are also highly conserved with their diffuse collateral projections retained as the telencephalon expands. In zebrafish, responses to predictive and factual threats involve brain structures that, despite inverted morphology,² control the same responses as in humans. These zebrafish reactions can be linked to anxiety (Mathuru & Jesuthasan, 2013). Likewise, the zebrafish can be used as a “reduced” model of a range of human emotional and cognitive disorders (de Abreu et al., 2020; Fontana et al., 2019; Gerlai, 2020; Soares, Gerlai & Maximino, 2018) .

PAG is a key structure for emotion generation. Even after hypothalamic and amygdala lesions, electrical stimulation of posterior/dorsal PAG in rats elicits escape reactions in the absence of external threat (de Molina & Hunsperger, 1962; Schreiner & Kling, 1953) – producing panic-like responses (Ballesteros, de Oliveira Galvão, Maisonette, & Landeira-Fernandez, 2014). This panic response to PAG stimulation is conserved in humans (Del-Ben & Graeff, 2009) and, similarly, depressed patients show irregular PAG functional connectivity (Truini et al., 2016).

PAG remains involved with more complex emotions. In healthy humans, social rejection increases activity in the dorsal anterior cingulate, amygdala, and PAG (Eisenberger, Gable, & Lieberman, 2007). In this hierarchy, higher levels control response production by interacting with the lower (Figure 1). Clearly, the PAG is where we should look for a neural sensitivity that gives rise

²Fish dorsal telencephalon is considered a homologue of the mammalian amygdala (Jesuthasan, 2012; Lal et al., 2018; Yamaguchi, Danjo, Pastan, Hikida, & Nakanishi, 2013).

to a panic-prone facet of personality or for basic panic psychopathology (that would couple with neuroticism to deliver panic disorder).

Above the PAG are the hypothalamus (archetypally associated with detailed motivational control), and the amygdala (Figure 1). The amygdala is complex, spans the subcortex and cortex, and is critical for the control of arousal with all motivations (Murray, 2007). Roughly one third of its neurons respond selectively to motivationally relevant stimuli in primates (Fuster & Uyeda, 1971). In all mammals, cortex and subcortex send positive and negative valence signals that the amygdala integrates to elicit adaptive behaviours via downstream targets (Correia & Goosens, 2016; McDonald, 1998; Smith & Torregrossa, 2021; Stefanacci & Amaral, 2002). Disruption in valence encoding is linked to the development of mood disorders in non-human models (Perusini & Fanselow, 2015) and humans (Brock, Harp, & Neta, 2022; Sequeira, Forbes, Hanson, & Silk, 2022).

In sum, fundamental aspects of emotional traits and of psychopathology are controlled in humans by conserved systems including diffuse ascending components that terminate throughout the neocortex (Dubois, Galdi, Han, Paul, & Adolphs, 2018; Dubois et al., 2020). This allows non-humans, from fish through primates, to provide meaningful models (with true homologies) of the core emotion production systems through which the complex sensory filters of more recently evolved cortical systems (Falcone et al., 2020; Miller, Hof, Sherwood, & Hopkins, 2021) change affect, behaviour, cognition, and desire. Both between and within species, trait aspects of these systems depend on genes and their interaction with the developmental environment of the organism. Here, in particular, non-human models are useful.

3. Genes, environment, and personality

Genes are a scaffold that constrains the external factors that mould emotion-processing circuits and so shape personality and psychopathology. Parental socioeconomic status, parenting practices, peer relationships, romantic relationships, and work experiences all affect personality traits (Ayoub & Roberts, 2017) and their stability into adulthood (Hopwood et al., 2011; Roberts & DelVecchio, 2000). Early-life adversity is a strong determinant of maladaptive personality in adults (de Carvalho et al., 2015; Perna, Vanni, Di Chiaro, Cavedini, & Caldirola, 2014; Rademaker, Vermetten, Geuze, Mulder, & Kleber, 2008; Schouw, Verkes, Schene & Schellekens, 2020). These trait effects depend on physiological alterations that include epigenetic modulation (Alshaya, 2022), HPA axis dysfunctionality (Lopez et al., 2021), and interruption of normal brain development (Marshall, Fox, & Group, 2004). Neither such environmental effects, related genes, nor their interaction can be thoroughly studied experimentally in humans. Here, non-human models are an important tool.

For example, chronic stress is thought to interact with genes to generate mood disorders in humans. “Carioca” rats, selectively bred to have high or low inherent anxiety responses allow us to assess the direction of the stress-anxiety association. Chronic unpredictable mild stress during development produces a greater increase in later reactions to threat in the high responding rats than in the low (Lages et al., 2021).

Environmental effects can also be studied in depth. For example, maternal separation in rodents and primates produces effects homologous to separation in humans. Macaques show that social factors are important (Kaufman & Rosenblum, 1969). Pigtail macaques live in small groups and their infants show strong separation

reactions, easily characterised as grief and severe depression. Bonnet macaques cluster in larger groups and their infants’ separation reaction, rather than strong distress, is to interact with other adults, generating solicitous behaviours including adoption. Rodents show that early adversity leads later in life to anxiety-like behaviours and increased stress responsiveness (Hegde & Mitra, 2020) in a sex- and age-dependent manner (Réus et al., 2021; Zanta, Suchecki, & Girardi, 2021) that can be enhanced by acute stress (Zanta et al., 2021) and ameliorated by an enriched environment (Réus et al., 2021).

Importantly for personality neuroscience, the amygdala, hippocampus, and endocrine system are substrates of these responses to early adversity (Ellis & Honeycutt, 2021; Qin et al., 2021) with similar brain changes apparent in humans (Pollok et al., 2022). The comparison of strain selection and environmental experiments in non-humans with confirmatory, albeit correlational, human imaging is a powerful solution to the problems facing each approach separately.

4. Cognition and personality

But what of more complex cognitive processes? While subcortex is substantially conserved between basal insectivores and humans, and archicortex (hippocampus) retains its basic structure and expands only moderately ($\times 4$), neocortex is greatly expanded ($\times 150$) and elaborated (Stephan & Andy, 1969). How far can rodent neocortex (and traits it controls) be seen as homologous to human?

The cortical elaboration of basic emotional traits operates to some extent through, and retains much of, primordial emotion control (the expansion of isocortex is functionally peripheral, with older allocortex in the deeper functional zones). Phylogeny layers fine-grain facet detail onto this primordium; elaborating species-specific expression of the same fundamental phenomena. Different triggers (via different sensory modalities and schemae) support innate simple phobias: the mouse fears the (smell of the) rat; the rat fears the (smell of the) cat; the human fears the (number of legs of the) spider. There are also species-specific responses (rats do not spray predators; while skunks do so with glands, and humans with cans of insecticide) but these trigger and effector differences are superficial. Prefrontal and cingulate cortex simply add the capacity for more complex, e.g., social, stimuli to generate clinically problematic panic that is nonetheless primitive. The fundamental internal reactions and control are much the same across all these species; with panicolytic drugs having the same functional effect, including with human social anxiety and obsessive-compulsive disorder (De Oliveira Sergio et al., 2020; Piccinelli, Pini, Bellantuono, & Wilkinson, 1995).

But when reflexive survival circuits or habitual reactions are insufficient to maintain goal-directed behaviour, they must be stopped, and more complex prefrontal control put in their place. For example, anterior cingulate cortex overcomes reflexive action generation and allocation of attention via processes that can be measured in simple behavioural tasks such as the stop-signal (SST), go/no-go, Stroop, and Eriksen flanker (Shackman et al., 2011). The SST is the simplest, designed to assess pure stopping (Logan, Cowan, & Davis, 1984). This simple “ability to suppress unwanted or inappropriate actions and impulses (‘response inhibition’) is a crucial component of flexible and goal-directed behavior . . . Its derailment is considered integral to numerous neurological and psychiatric disorders, and more generally, to a wide range of behavioral and health problems.” (Verbruggen et al., 2019, p. 2 . . . p. 1).

The neural basis of stopping is well studied and involves, in particular, the right inferior frontal gyrus in humans – homologous to the orbital frontal area in rats (Aron, Robbins, & Poldrack, 2014). Interestingly, in humans in the SST, a distinct goal-conflict-related right frontal activation (Shadli, Glue, McIntosh, & McNaughton, 2015; Shadli et al., 2020) is a biomarker for anxiety disorder (Shadli et al., 2021) and is inversely linked to Attention Deficit Hyperactivity Disorder (ADHD; Sadeghi et al., 2018). In rats in the SST (a case of inverse translation), the same goal conflict activation involves homologous circuitry including the orbital frontal area, hippocampus, and subthalamus (Banstola, Young, Parr-Brownlie, & McNaughton, 2022). Thus, in stimulus terms, *why* a human chooses to stop differs across occasions and may differ from why a rat does; but *how* rats and humans stop appears to be the same; and stop-go conflict engages homologous parallel circuits that are involved in trait psychopathologies that are occasion-general.

Likewise, rat models of ADHD (with attentional and inhibition deficits across multiple tests) have elucidated dopaminergic and noradrenergic mechanisms (Bayless, Perez, & Daniel, 2015; Li et al., 2021; Russell, Allie, & Wiggins, 2000; Sable et al., 2021). Comparison of two such models (the Spontaneously Hypertensive rat and the New Zealand Genetically Hypertensive rat) in a modified child delayed reinforcement “marshmallow” test allowed a nuanced test of the likely control of immediate reinforcement in ADHD (Sutherland et al., 2009).

Cortical involvement is not all top-down. Emotions impact cognitive control. Emotional stimuli disrupt inhibition in humans (Kalanthoff, Cohen, & Henik, 2013; Pessoa, Padmala, Kenner, & Bauer, 2012) and non-humans (Kambali, Anshu, Kuty, Muddashetty, & Laxmi, 2019; Klein et al., 2014; Weimar et al., 2020) and disrupt working memory (Bishop, 2007; Bishop & Forster, 2013; Etkin, 2012; Etkin, Gyurak, & O'Hara, 2013; Okon-Singer et al., 2014; van Ast et al., 2016). Emotionally relevant distractors impact task performance via (1) increased activity of ventral brain structures associated with emotional processing, such as the amygdala and ventral prefrontal cortex and (2) decreased activity of dorsal regions involved with executive processing, such as the dorsolateral prefrontal cortex and lateral parietal cortex (Jordan, Dolcos, & Dolcos, 2013). Emotional recovery, neuroticism, and chronic stress are intermingled and associated with disruption in these systems (Blackford, Avery, Shelton, & Zald, 2009; Lapate et al., 2014; Schuyler et al., 2014).

Again, non-human translational models are available. For example, Yee, Leng, Shenhav and Braver (2022) showed how the manipulation of reward and punishment in different rodent models of conditioning tasks may demonstrate whether the presence of the aversive stimulus strengthens or weakens behaviour. Similar tasks in primates confirmed the importance of different regions of the frontal, parietal, and cingulate cortex (Amemori, Amemori, & Graybiel, 2015; Amemori & Graybiel, 2012; Leathers & Olson, 2012) in emotional-motivated decision making (Roesch & Olson, 2004).

Despite all these homologies, there are likely to be some who question the idea of non-human cognition, in and of itself. We have argued against the

anthropocentric fallacies underlie the separation of biological and cognitive constructs in psychology in general and personality psychology in particular. . . . The [counter] arguments adhere to two fundamental beliefs in biology: the continuity of species implied by Darwinian evolution; and the mapping of mind to brain as different levels of description of the same fundamental entity. Mind is not here identical to brain. It is a property of brain processes. . . . The human species is, of course, unique. . . . But no character sets us apart from other animals in a way that other characters do not set each species apart from all others.” (McNaughton & Corr, 2008, pp. 95–101)

There are strong reasons, here, to reject radical behaviourism, primary anthropocentrism, cognitive anthropocentrism; and the ideas that cognitions are: language-dependent; emotionally neutral; unconstrained; hardware-free; silent; and seated in the cortex (McNaughton & Corr, 2008).

5. Personality and psychopathology

Latzman, Krueger, DeYoung and Michelini (2021) describe distinct approaches to personality and psychopathology. Personality is viewed dimensionally; but psychopathology is often viewed categorically. However, critical limitations exist in the categorical models of psychopathology (Cuthbert, 2015; Krueger et al., 2018). Instead, empirical evidence favours continuous/dimensional perspectives, such as the MMPI/Minnesota Multiphasic Personality Inventory (Ben-Porath & Tellegen, 2008/2011). “The MMPI has evolved from an innovation that was developed via state-of-the-art procedures in the 1930s into the current MMPI-2-RF that is psychometrically up to date and aligns well with contemporary models of psychopathology. . . . The MMPI-2-RF substantive scales operationalize psychological constructs that are dimensional and transdiagnostic in nature. The MMPI-2-RF scales map onto the promising HiTOP model, which represents a recent, comprehensive effort to organize psychopathology in a hierarchical and dimensional manner” (Sellbom, 2019, p. 169–170). HiTOP/The Hierarchical Taxonomy of Psychopathology initiative “constructs psychopathological syndromes and their components/subtypes based on the observed covariation of symptoms, [and] combines co-occurring syndromes into spectra, thereby mapping out comorbidity” (Kotov et al., 2017, 2021). Thus, “quantitatively derived, integrative models of personality–psychopathology represent a particularly promising conduit for advancing our understanding of the neurobiological foundation of human experience, both functional and dysfunctional” (Latzman et al., 2021, p. 1).

According to Widiger (2011), the relationship of personality and psychopathology can be approached in three different ways: (1) personality and psychopathology can influence the presentation or appearance of one another; (2) they can share a common, underlying aetiology; or (3) they can have a causal role in the development or aetiology of one another. Empirical evidence in support of the first approach shows, for example, the presence of personality traits of perfectionism and compulsivity in persons with anorexia and impulsivity in those with bulimic symptomatology (Cassin & von Ranson, 2005). On the other hand, while persons high in neuroticism will respond to stress with clinically significant levels of depression, this following depression would lead the patients to provide a distorted description of their usual way of thinking, feeling, behaving, and relating to others, i.e., dimensions of personality (Gunderson et al., 2003). This change in self-report following a mood disorder can be argued to pose as an actual change in personality (Costa, Bagby, Herbst, & McCrae, 2005; Widiger, 2011).

“claim that emotion and personality, nonetheless, remain distinct from the rest of biology; that with them it is still the case that ‘the only proper study of mankind is man’ . . . [with] the role of ‘pure cognition’ as so central to human psychology as to make biology irrelevant, or at least a second-best level of analysis. . . . We suspect that [a range of essentially

The difficulty of isolating or manipulating the relevant variables in human studies limits understanding of the relationship between personality and psychopathology. Non-human models, then, provide a tool for the analysis of the various genetic, environmental, or pharmacological influences underlying the behavioural expression and physiological functions homologous in non-humans and humans (Kumar, Bhat, & Kumar, 2013). Based on face, predictive, and construct validities, these models have contributed to elucidating different aspects of various psychiatric disorders, such as anxiety, depression, and PTSD (Abelaira, Réus, & Quevedo, 2013; Buenhombre, Daza-Cardona, Sousa, & Gouveia, 2021; Campos, Fogaça, Aguiar, & Guimarães, 2013; Dunsmoor, Cisler, Fonzo, Creech, & Nemeroff, 2022; Gomes Vitor de Castro et al., 2013), autism (Chadman, 2017; Varghese et al., 2017), compulsive eating (Di Segni, Patrono, Patella, Puglisi-Allegra, & Ventura, 2014; Turton, Chami, & Treasure, 2017), and schizophrenia (Jones, Watson, & Fone, 2011; Winship et al., 2018).

6. Conclusions

In sum, there is good reason to see non-human models as providing a range of “reduced” examples of the fundamental neural control of emotional (and other psychological) traits. Importantly, these fundamental systems are highly conserved functionally and neurally; with neocortical expansion simply adding superficial complexity to their trigger stimuli and effector outputs. Selection of non-human strains provides an experimental means to answer questions about genes, environment, and their interactions in shaping personality. Non-human models also clearly apply to cognitive as well as emotional traits provided care is taken to determine the relevant neural and behavioural homologies. Finally, in an era where personality and psychopathology are moving to a common integration, non-human models (particularly of psychiatric disorders) provide a means of mapping out the neural bedrock that must be common to both healthy and disordered personality.

We hope this Special Issue will help convince those who construct human personality questionnaires to look to non-human work (particularly neuroscience) as a basis for both construction and validation. There will also always be those who think that their non-human studies cannot, even should not, be used to develop human personality questionnaires. But our main goal is human personality psychology! This raises the issue of how we translate between animal experimental studies and human personality questionnaires.

Such translation is not a new idea. For example, Eysenck’s early human work led to development of the Maudsley rat strains as a model of emotionality or neuroticism (Blizard & Adams, 2002). In the reverse direction, non-human work, via the idea of a Conceptual Nervous System (Gray, 1972a; Hebb, 1955), provided the impetus for the Reinforcement Sensitivity Theory of Personality (Corr, 2008; Gray, 1972b).

But we suggest that such translational work can be deeper. Only a partial connection with non-human and neural bedrock was made, primarily at the scale-construction stage, in development of RST scales (Carver & White, 1994; Wilson, Barrett, & Gray, 1989; Wilson, Gray, & Barrett, 1990), Affective Neuroscience Personality Scales (Davis & Panksepp, 2018; Davis, Panksepp, & Normansell, 2003; Montag, Elhai, & Davis, 2021), and the Tridimensional Personality Questionnaire (Cloninger, 1987; Cloninger, Przybeck, & Svrakic, 1991). These scales used fundamental neurobiology for the theoretical model stage of scale

development but used conventional item pool generation and structural validation (Clark & Watson, 2019) to generate linguistically complex items. In some cases, this led to malleable constructs – PANIC in one version of the Affective Neuroscience Personality Scales was later changed to SADNESS on purely semantic grounds (Davis et al., 2003). However, such questionnaires (derived from and interpreted through non-human data) have seldom been directly validated against homologous behavioural or neural measures to those of the original base theories.

With modern developments in genetics, imaging, and translational biomarker development (Shadli et al., 2021), there is now scope for deeper connections to be made and for questionnaire constructs to be validated via neurobiology. Tests using virtual worlds with real-world consequences can link human trait measures to essentially the same behaviours as those measured in non-human tests (Bach et al., 2014; Fung, Qi, Hassabis, Daw, & Mobbs, 2019; Korn & Bach, 2019). Importantly, imaging in these virtual world human tests demonstrates essentially the same neural architecture as detailed in a mass of previous non-human work (McNaughton, 2019). We expect the papers in this Special Issue to open up many such avenues, with traffic flowing in both directions.

Acknowledgments. This work was supported by CNPq (The National Council for Scientific and Technological Development of Brazil).

Conflicts of interest. None.

References

- Abelaira, H. M., Réus, G. Z., & Quevedo, J. (2013). Animal models as tools to study the pathophysiology of depression. *Brazilian Journal of Psychiatry*, 35(Suppl 2), S112–S120. <https://doi.org/10.1590/1516-4446-2013-1098>
- Alshaya, D. S. (2022). Genetic and epigenetic factors associated with depression: An updated overview. *Saudi Journal of Biological Sciences*, 29, 103311. <https://doi.org/10.1016/j.sjbs.2022.103311>
- Altschul, D., Robinson, L., Coleman, K., Capitanio, J. P., & Wilson, V. (2019). An exploration of the relationships among facial dimensions, age, sex, dominance status, and personality in rhesus macaques (*Macaca mulatta*). *International Journal of Primatology*, 40, 532–552. <https://doi.org/10.1007/s10764-019-00104-y>
- Amemori, K.-i., Amemori, S., & Graybiel, A. M. (2015). Motivation and affective judgments differentially recruit neurons in the primate dorsolateral prefrontal and anterior cingulate cortex. *The Journal of Neuroscience*, 35, 1939–1953. <https://doi.org/10.1523/jneurosci.1731-14.2015>
- Amemori, K.-i., & Graybiel, A. M. (2012). Localized microstimulation of primate pregenual cingulate cortex induces negative decision-making. *Nature Neuroscience*, 15, 776–785. <https://doi.org/10.1038/nn.3088>
- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2014). Inhibition and the right inferior frontal cortex: One decade on. *Trends in Cognitive Sciences*, 18, 177–185. <https://doi.org/10.1016/j.tics.2013.12.003>
- Ayoub, M., & Roberts, B. W. (2017). Environmental conditions and the development of personality. In V. Zeigler-Hill & T. K. Shackelford (Eds.), *Encyclopedia of personality and individual differences* (pp. 1–9). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-28099-8_1859-1
- Bach, D. R., Guitart-Masip, M., Packard, P. A., Miro, J., Falip, M., Fuentesmilla, L., & Dolan, R. J. (2014). Human hippocampus arbitrates approach-avoidance conflict. *Current Biology*, 24, 541–547. <https://doi.org/10.1016/j.cub.2014.01.046>
- Ballesteros, C. I., de Oliveira Galvão, B., Maisonette, S., & Landeira-Fernandez, J. (2014). Effect of dorsal and ventral hippocampal lesions on contextual fear conditioning and unconditioned defensive behavior induced by electrical stimulation of the dorsal periaqueductal gray. *PLOS ONE*, 9, e83342. <https://doi.org/10.1371/journal.pone.0083342>

- Banstola, A., Young, C. K., Parr-Brownlie, L., & McNaughton, N.** (2022). Dynamic interaction between hippocampus, orbitofrontal cortex, and subthalamic nucleus during goal conflict in the stop signal task in rats. *Neuroscience Research*, *182*, 65–75. <https://doi.org/10.1016/j.neures.2022.06.006>
- Barrett, L. F.** (2017). *How emotions are made: The secret life of the brain*. Boston, MA: Houghton Mifflin Harcourt.
- Bayless, D. W., Perez, M. C., & Daniel, J. M.** (2015). Comparison of the validity of the use of the spontaneously hypertensive rat as a model of attention deficit hyperactivity disorder in males and females. *Behavioural Brain Research*, *286*, 85–92. <https://doi.org/10.1016/j.bbr.2015.02.029>
- Ben-Porath, Y. S., & Tellegen, A.** (2008/2011). *MMPI-2-RF (Minnesota Multiphasic Personality Inventory-2 Restructured Form): Manual for administration, scoring, and interpretation*. Minneapolis, MN: University of Minnesota Press.
- Bishop, S.** (2007). Neurocognitive mechanisms of anxiety: An integrative account. *Trends in Cognitive Sciences*, *11*, 307–316. <https://doi.org/10.1016/j.tics.2007.05.008>
- Bishop, S., & Forster, S.** (2013). Trait anxiety, neuroticism, and the brain basis of vulnerability to affective disorder. In J. Armony & P. Vuilleumier (Eds.), *The Cambridge handbook of human affective neuroscience* (pp. 553–574). Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511843716.031>
- Blackford, J. U., Avery, S. N., Shelton, R. C., & Zald, D. H.** (2009). Amygdala temporal dynamics: Temperamental differences in the timing of amygdala response to familiar and novel faces. *BMC Neuroscience*, *10*, 145. <https://doi.org/10.1186/1471-2202-10-145>
- Blanchard, R. J., & Blanchard, D. C.** (1989). Attack and defense in rodents as ethoexperimental models for the study of emotion. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *13*, S3–S14. [https://doi.org/10.1016/0278-5846\(89\)90105-X](https://doi.org/10.1016/0278-5846(89)90105-X)
- Blizard, D. A., & Adams, N.** (2002). The Maudsley Reactive and Nonreactive strains: A new perspective. *Behavior Genetics*, *32*, 277–299. <https://doi.org/10.1023/A:1020206120248>
- Brock, R. L., Harp, N. R., & Neta, M.** (2022). Interpersonal emotion regulation mitigates the link between trait neuroticism and a more negative valence bias. *Personality and Individual Differences*, *196*, 111726. <https://doi.org/10.1016/j.paid.2022.111726>
- Buenhombre, J., Daza-Cardona, E. A., Sousa, P., & Gouveia, A.** (2021). Different influences of anxiety models, environmental enrichment, standard conditions and intraspecies variation (sex, personality and strain) on stress and quality of life in adult and juvenile zebrafish: A systematic review. *Neuroscience & Biobehavioral Reviews*, *131*, 765–791. <https://doi.org/10.1016/j.neubiorev.2021.09.047>
- Campos, A. C., Fogaça, M. V., Aguiar, D. C., & Guimarães, F. S.** (2013). Animal models of anxiety disorders and stress. *Brazilian Journal of Psychiatry*, *35*(Suppl 2), S101–S111. <https://doi.org/10.1590/1516-4446-2013-1139>
- Carver, C., & White, T.** (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. *Journal of Personality and Social Psychology*, *67*, 319–333. <https://doi.org/10.1037/0022-3514.67.2.319>
- Cassin, S. E., & von Ranson, K. M.** (2005). Personality and eating disorders: A decade in review. *Clinical Psychology Review*, *25*, 895–916. <https://doi.org/10.1016/j.cpr.2005.04.012>
- Chadman, K. K.** (2017). Animal models for autism in 2017 and the consequential implications to drug discovery. *Expert Opinion on Drug Discovery*, *12*, 1187–1194. <https://doi.org/10.1080/17460441.2017.1383982>
- Clark, L. A., & Watson, D.** (2019). Constructing validity: New developments in creating objective measuring instruments. *Psychological Assessment*, *31*, 1412–1427. <https://doi.org/10.1037/pas0000626>
- Cloninger, C. R.** (1987). A systematic method for clinical description and classification of personality variants: A proposal. *Archives of General Psychiatry*, *44*, 573–588. <https://doi.org/10.1001/archpsyc.1987.01800180093014>
- Cloninger, C. R., Przybeck, T. R., & Svrakic, D. M.** (1991). The tridimensional personality questionnaire: U.S. normative data. *Psychological Reports*, *69*, 1047–1057. <https://doi.org/10.2466/pr0.1991.69.3.1047>
- Comoli, E., Ribeiro-Barbosa, E. R., & Canteras, N. S.** (2003). Predatory hunting and exposure to a live predator induce opposite patterns of Fos immunoreactivity in the PAG. *Behavioural Brain Research*, *138*, 17–28. [https://doi.org/10.1016/S0166-4328\(02\)00197-3](https://doi.org/10.1016/S0166-4328(02)00197-3)
- Corr, P. J.** (2008). *The reinforcement sensitivity theory of personality*. Cambridge: Cambridge University Press.
- Correia, S. S., & Goossens, K. A.** (2016). Input-specific contributions to valence processing in the amygdala. *Learning & Memory*, *23*, 534–543. <https://doi.org/10.1101/lm.037887.114>
- Costa, P. T., Bagby, R. M., Herbst, J. H., & McCrae, R. R.** (2005). Personality self-reports are concurrently reliable and valid during acute depressive episodes. *Journal of Affective Disorders*, *89*, 45–55. <https://doi.org/10.1016/j.jad.2005.06.010>
- Cuthbert, B. N.** (2015). Research Domain Criteria: Toward future psychiatric nosologies. *Dialogues in Clinical Neuroscience*, *17*, 89–97. <https://doi.org/10.31887/DCNS.2015.17.1/bcuthbert>
- Darwin, C.** (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- Darwin, C.** (1871). *The descent of man, and selection in relation to sex*. London: John Murray.
- Darwin, C.** (1872). *The expression of the emotions in man and animals*. London: John Murray.
- Davis, K. L., & Panksepp, J.** (2018). *The emotional foundations of personality: A neurobiological and evolutionary approach*. New York: W. W. Norton & Co.
- Davis, K. L., Panksepp, J., & Normansell, L.** (2003). The affective neuroscience personality scales: Normative data and implications. *Neuropsychanalysis*, *5*, 57–69. <https://doi.org/10.1080/15294145.2003.10773410>
- de Abreu, M. S., Genario, R., Giacomini, A. C. V. V., Demin, K. A., Lakstygala, A. M., Amstislavskaya, T. G., ... Kalueff, A. V.** (2020). Zebrafish as a model of neurodevelopmental disorders. *Neuroscience*, *445*, 3–11. <https://doi.org/10.1016/j.neuroscience.2019.08.034>
- de Carvalho, H. W., Pereira, R., Frozi, J., Bisol, L. W., Ottoni, G. L., & Lara, D. R.** (2015). Childhood trauma is associated with maladaptive personality traits. *Child Abuse & Neglect*, *44*, 18–25. <https://doi.org/10.1016/j.chiabu.2014.10.013>
- de Molina, A. F., & Hunsperger, R. W.** (1962). Organization of the subcortical system governing defence and flight reactions in the cat. *The Journal of Physiology*, *160*, 200–213. <https://doi.org/10.1113/jphysiol.1962.sp006841>
- De Oliveira Sergio, T., Frias, A. T., Vilela-Costa, H. H., De Oliveira, D. C. G., Zuardi, A. W., & Zangrossi, H.** (2020). Serotonin mediates the panicolytic-like effect of oxytocin in the dorsal periaqueductal gray. *Journal of Psychopharmacology*, *34*, 383–390. <https://doi.org/10.1177/0269881120907960>
- Del-Ben, C. M., & Graeff, F. G.** (2009). Panic disorder: Is the PAG involved? *Neural Plasticity*, *2009*, 108135. <https://doi.org/10.1155/2009/108135>
- Di Segni, M., Patrono, E., Patella, L., Puglisi-Allegra, S., & Ventura, R.** (2014). Animal models of compulsive eating behavior. *Nutrients*, *6*, 4591–4609. <https://doi.org/10.3390/nu6104591>
- Dubois, J., Galdi, P., Han, Y., Paul, L. K., & Adolphs, R.** (2018). Resting-state functional brain connectivity best predicts the personality dimension of openness to experience. *Personality Neuroscience*, *1*, e6. <https://doi.org/10.1017/pen.2018.8>
- Dubois, J., Oya, H., Tyszka, J. M., Howard, M., Eberhardt, F., & Adolphs, R.** (2020). Causal mapping of emotion networks in the human brain: Framework and initial findings. *Neuropsychologia*, *145*, 106571. <https://doi.org/10.1016/j.neuropsychologia.2017.11.015>
- Dunsmoor, J. E., Cisler, J. M., Fonzo, G. A., Creech, S. K., & Nemeroff, C. B.** (2022). Laboratory models of post-traumatic stress disorder: The elusive bridge to translation. *Neuron*, *110*, 1754–1776. <https://doi.org/10.1016/j.neuron.2022.03.001>
- Eisenberger, N. I., Gable, S. L., & Lieberman, M. D.** (2007). Functional magnetic resonance imaging responses relate to differences in real-world social experience. *Emotion*, *7*, 745–754. <https://doi.org/10.1037/1528-3542.7.4.745>
- Ekman, P.** (1992). An argument for basic emotions. *Cognition and Emotion*, *6*, 169–200. <https://doi.org/10.1080/02699939208411068>
- Ellis, S. N., & Honeycutt, J. A.** (2021). Sex differences in affective dysfunction and alterations in parvalbumin in rodent models of early life adversity. *Frontiers in Behavioral Neuroscience*, *15*, 303. <https://doi.org/10.3389/fnbeh.2021.741454>

- Etkin, A. (2012). Neurobiology of anxiety: From neural circuits to novel solutions? *Depression and Anxiety*, 29, 355–358. <https://doi.org/10.1002/da.21957>
- Etkin, A., Gyurak, A., & O'Hara, R. (2013). A neurobiological approach to the cognitive deficits of psychiatric disorders. *Dialogues in Clinical Neuroscience*, 15, 419–429. <https://doi.org/10.31887/DCNS.2013.15.4/aetkin>
- Falcone, C., Penna, E., Hong, T., Tarantal, A. F., Hof, P. R., Hopkins, W. D., ... Martínez-Cerdeño, V. (2020). Cortical interlaminar astrocytes are generated prenatally, mature postnatally, and express unique markers in human and nonhuman primates. *Cerebral Cortex*, 31, 379–395. <https://doi.org/10.1093/cercor/bhaa231>
- Fontana, B. D., Franscescon, F., Rosemberg, D. B., Norton, W. H. J., Kalueff, A. V., & Parker, M. O. (2019). Zebrafish models for attention deficit hyperactivity disorder (ADHD). *Neuroscience & Biobehavioral Reviews*, 100, 9–18. <https://doi.org/10.1016/j.neubiorev.2019.02.009>
- Fung, B. J., Qi, S., Hassabis, D., Daw, N., & Mobbs, D. (2019). Slow escape decisions are swayed by trait anxiety. *Nature Human Behaviour*, 3, 702–708. <https://doi.org/10.1038/s41562-019-0595-5>
- Fuster, J. M., & Uyeda, A. A. (1971). Reactivity of limbic neurons of the monkey to appetitive and aversive signals. *Electroencephalography and Clinical Neurophysiology*, 30, 281–293. [https://doi.org/10.1016/0013-4694\(71\)90111-8](https://doi.org/10.1016/0013-4694(71)90111-8)
- Gerlai, R. T. (2020). Relational learning in zebrafish: A model of declarative memory in humans?. In R. T. Gerlai (Ed.), *Behavioral and neural genetics of zebrafish* (pp. 205–220). London: Academic Press. <https://doi.org/10.1016/B978-0-12-817528-6.00013-9>
- Gomes, V. C., Hassan, W., Maisonnette, S., Johnson, L. R., Ramos, A., & Landeira-Fernandez, J. (2013). Behavioral evaluation of eight rat lines selected for high and low anxiety-related responses. *Behavioral Brain Research*, 257, 39–48. <https://doi.org/10.1016/j.bbr.2013.09.028>
- Gray, J. A. (1972a). Learning theory, the conceptual nervous system and personality. In V. D. Nebllytsyn & J. A. Gray (Eds.), *The biological bases of individual behaviour* (pp. 372–399). London/New York: Academic Press.
- Gray, J. A. (1972b). The psychophysiological nature of introversion-extraversion: A modification of Eysenck's theory. In V. D. Nebllytsyn & J. A. Gray (Eds.), *The biological bases of individual behaviour* (pp. 182–205). London/New York: Academic Press.
- Greene, D. J., Marek, S., Gordon, E. M., Siegel, J. S., Gratton, C., Laumann, T. O., ... Dosenbach, N. U. F. (2020). Integrative and network-specific connectivity of the basal ganglia and thalamus defined in individuals. *Neuron*, 105, 742–758.e746. <https://doi.org/https://doi.org/10.1016/j.neuron.2019.11.012>
- Gunderson, J. G., Bender, D., Sanislow, C., Yen, S., Rettew, J. B., Dolan-Sewell, R., ... Skodol, A. E. (2003). Plausibility and possible determinants of sudden, remissions, in borderline patients. *Psychiatry: Interpersonal and Biological Processes*, 66, 111–119. <https://doi.org/10.1521/psyc.66.2.111.20614>
- Hebb, D. O. (1955). Drives and the C.N.S. (conceptual nervous system). *Psychological Review*, 62, 243–254.
- Hegde, A., & Mitra, R. (2020). Environment and early life: Decisive factors for stress-resilience and vulnerability. In A. Clow & N. Smyth (Eds.), *International review of neurobiology* (Vol. 150, pp. 155–185). New York: Academic Press. <https://doi.org/10.1016/bs.irm.2019.12.002>
- Hones, V. I., & Mizumori, S. J. Y. (2022). Response flexibility: The role of the lateral habenula. *Frontiers in Behavioral Neuroscience*, 16, 112471. <https://doi.org/10.3389/fnbeh.2022.852235>
- Hopwood, C. J., Donnellan, M. B., Blonigen, D. M., Krueger, R. F., McGue, M., Iacono, W. G., & Burt, S. A. (2011). Genetic and environmental influences on personality trait stability and growth during the transition to adulthood: A three-wave longitudinal study. *Journal of Personality and Social Psychology*, 100, 545–556. <https://doi.org/10.1037/a0022409>
- Jordan, A., Dolcos, S., & Dolcos, F. (2013). Neural signatures of the response to emotional distraction: A review of evidence from brain imaging investigations. *Frontiers in Human Neuroscience*, 7, 200. <https://doi.org/10.3389/fnhum.2013.00200>
- James, W. (1884). What is an emotion? *Mind*, 9, 188–205.
- Janacek, K., Evans, T. M., Kiss, M., Shah, L., Blumenfeld, H., & Ullman, M. T. (2022). Subcortical cognition: The fruit below the rind. *Annual Review of Neuroscience*, 45, 361–386. <https://doi.org/10.1146/annurev-neuro-110920-013544>
- Jesuthasan, S. (2012). Fear, anxiety, and control in the zebrafish. *Developmental Neurobiology*, 72, 395–403. <https://doi.org/10.1002/dneu.20873>
- Jones, C., Watson, D., & Fone, K. (2011). Animal models of schizophrenia. *British Journal of Pharmacology*, 164, 1162–1194. <https://doi.org/10.1111/j.1476-5381.2011.01386.x>
- Kalanthroff, E., Cohen, N., & Henik, A. (2013). Stop feeling: Inhibition of emotional interference following stop-signal trials. *Frontiers in Human Neuroscience*, 7, 78. <https://doi.org/10.3389/fnhum.2013.00078>
- Kambali, M. Y., Anshu, K., Kuttly, B. M., Muddashetty, R. S., & Laxmi, T. R. (2019). Effect of early maternal separation stress on attention, spatial learning and social interaction behaviour. *Experimental Brain Research*, 237, 1993–2010. <https://doi.org/10.1007/s00221-019-05567-2>
- Kaufman, I. C., & Rosenblum, L. A. (1969). Effects of separation from mother on the emotional behaviour of infant monkeys. *New York Academy of Science*, 159, 681–695.
- Keay, K. A., & Bandler, R. (2015). Periaqueductal gray. In G. Paxinos (Ed.), *The rat nervous system* (4th ed., pp. 207–221). San Diego: Academic Press. <https://doi.org/10.1016/B978-0-12-374245-2.00010-3>
- Klein, A. B., Ultved, L., Adamsen, D., Santini, M. A., Tobeña, A., Fernandez-Teruel, A., ... Mikkelsen, J. D. (2014). 5-HT(2A) and mGlu2 receptor binding levels are related to differences in impulsive behavior in the Roman Low- (RLA) and High- (RHA) avoidance rat strains. *Neuroscience*, 263, 36–45. <https://doi.org/10.1016/j.neuroscience.2013.12.063>
- Korn, C. W., & Bach, D. R. (2019). Minimizing threat via heuristic and optimal policies recruits hippocampus and medial prefrontal cortex. *Nature Human Behaviour*, 3, 733–745. <https://doi.org/10.1038/s41562-019-0603-9>
- Kotov, R., Krueger, R. F., Watson, D., Achenbach, T., Althoff, R. R., Bagby, R. M., ... Zimmerman, M. (2017). The Hierarchical Taxonomy of Psychopathology (HiTOP): A dimensional alternative to traditional nosologies. *Journal of Abnormal Psychology*, 126, 454–477. <https://doi.org/10.1037/abn0000258>
- Kotov, R., Krueger, R. F., Watson, D., Cicero, D. C., Conway, C. C., DeYoung, C. G., ... Wright, A. G. C. (2021). The Hierarchical Taxonomy of Psychopathology (HiTOP): A quantitative nosology based on consensus of evidence. *Annual Review of Clinical Psychology*, 17, 83–108. <https://doi.org/10.1146/annurev-clinpsy-081219-093304>
- Krueger, R. F., Kotov, R., Watson, D., Forbes, M. K., Eaton, N. R., Ruggero, C. J., ... Zimmermann, J. (2018). Progress in achieving quantitative classification of psychopathology. *World Psychiatry*, 17, 282–293. <https://doi.org/10.1002/wps.20566>
- Kumar, V., Bhat, Z. A., & Kumar, D. (2013). Animal models of anxiety: A comprehensive review. *Journal of Pharmacological and Toxicological*, 68, 175–183. <https://doi.org/10.1016/j.vascn.2013.05.003>
- Kyuhou, S. L., & Gemba, H. (1998). Two vocalization-related subregions in the midbrain periaqueductal gray of the guinea pig. *NeuroReport*, 9, 1607–1610. <https://doi.org/10.1097/00001756-199805110-00064>
- Lages, Y. V., Maisonnette, S. S., Marinho, B., Rosseti, F. P., Krahe, T. E., & Landeira-Fernandez, J. (2021). Behavioral effects of chronic stress in Carioca high- and low-conditioned freezing rats. *Stress*, 24, 1–10. <https://doi.org/10.1080/10253890.2021.1934445>
- Lal, P., Tanabe, H., Suster, M. L., Ailani, D., Kotani, Y., Muto, A., ... Kawakami, K. (2018). Identification of a neuronal population in the telencephalon essential for fear conditioning in zebrafish. *BMC Biology*, 16, 45. <https://doi.org/10.1186/s12915-018-0502-y>
- Lapate, R. C., van Reekum, C. M., Schaefer, S. M., Greischar, L. L., Norris, C. J., Bachhuber, D. R. W., ... Davidson, R. J. (2014). Prolonged marital stress is associated with short-lived responses to positive stimuli. *Psychophysiology*, 51, 499–509. <https://doi.org/10.1111/psyp.12203>
- Latzman, R. D., Krueger, R. F., DeYoung, C. G., & Michelini, G. (2021). Connecting quantitatively derived personality-psychopathology models and neuroscience. *Personality Neuroscience*, 4, e4. <https://doi.org/10.1017/pen.2021.3>
- Leathers, M. L., & Olson, C. R. (2012). In monkeys making value-based decisions, lip neurons encode cue salience and not action value. *Science*, 338, 132–135. <https://doi.org/10.1126/science.1226405>

- Ledoux, J.** (1991). Emotion and the limbic system concept. *Concepts in Neuroscience*, 2, 169–199.
- LeDoux, J.** (1996). Emotional networks and motor control: A fearful view. In G. Holstege, R. Bandler & C. B. Saper (Eds.), *Progress in brain research* (Vol. 107, pp. 437–446). Amsterdam: Elsevier. [https://doi.org/10.1016/S0079-6123\(08\)61880-4](https://doi.org/10.1016/S0079-6123(08)61880-4)
- Ledoux, J.** (2012). Emotional colouration of consciousness: How feelings come about. In L. Weiskrantz & M. Davies (Eds.), *Frontiers of consciousness: Chichele lectures*. Oxford: Oxford Academic. <https://doi.org/10.1093/acprof:oso/9780199233151.003.0003>
- Li, J.-S., Yang, S.-S., Huston, J. P., Chao, O. Y., Yang, Y.-M., & Mattern, C.** (2021). Acute intranasal dopamine application counteracts the reversal learning deficit of spontaneously hypertensive rats in an attentional set-shifting task. *Psychopharmacology*, 238, 2419–2428. <https://doi.org/10.1007/s00213-021-05863-2>
- Logan, G. D., Cowan, W. B., & Davis, K. A.** (1984). On the ability to inhibit simple and choice reaction-time responses: A model and a method. *Journal of Experimental Psychology: Human Perception and Performance*, 10, 276–291. <https://doi.org/10.1037/0096-1523.10.2.276>
- Loonen, A. J. M., & Ivanova, S. A.** (2015). Circuits regulating pleasure and happiness: The evolution of reward-seeking and misery-fleeing behavioral mechanisms in vertebrates. *Frontiers in Neuroscience*, 9, 213. <https://doi.org/10.3389/fnins.2015.00394>
- Loonen, A. J. M., & Ivanova, S. A.** (2016). Circuits regulating pleasure and happiness: The evolution of the amygdalar-hippocampal-habenular connectivity in vertebrates. *Frontiers in Neuroscience*, 10, 1213. <https://doi.org/10.3389/fnins.2016.00539>
- Loonen, A. J. M., & Ivanova, S. A.** (2019). Evolution of circuits regulating pleasure and happiness with the habenula in control. *CNS Spectrums*, 24, 233–238. <https://doi.org/10.1017/S1092852917000748>
- Lopes da Silva, F. H., Witter, M. P., Boeijinga, P. H., & Lohman, A. H.** (1990). Anatomic organization and physiology of the limbic cortex. *Physiological Reviews*, 70, 453–511. <https://doi.org/10.1152/physrev.1990.70.2.453>
- Lopez, M., Ruiz, M. O., Rovnaghi, C. R., Tam, G. K. Y., Hiscox, J., Gotlib, I. H., . . . Anand, K. J. S.** (2021). The social ecology of childhood and early life adversity. *Pediatric Research*, 89, 353–367. <https://doi.org/10.1038/s41390-020-01264-x>
- MacLean, P. D.** (1949). Psychosomatic disease and the “visceral brain”: Recent developments bearing on the papez theory of emotion. *Psychosomatic Medicine*, 11, 338–353. <https://doi.org/10.1097/00006842-194911000-00003>
- MacLean, P. D.** (1952). Some psychiatric implications of physiological studies on frontotemporal portion of limbic system (Visceral brain). *Electroencephalography and Clinical Neurophysiology*, 4, 407–418. [https://doi.org/10.1016/0013-4694\(52\)90073-4](https://doi.org/10.1016/0013-4694(52)90073-4)
- Marshall, P. J., Fox, N. A., & Group, B. C.** (2004). A comparison of the electroencephalogram between institutionalized and community children in Romania. *Journal of Cognitive Neuroscience*, 16, 1327–1338. <https://doi.org/10.1162/0898929042304723>
- Mathuru, A. S., & Jesuthasan, S.** (2013). The medial habenula as a regulator of anxiety in adult zebrafish. *Frontiers in Neural Circuits*, 7, Article 99. <https://doi.org/10.3389/fncir.2013.00099>
- McDonald, A. J.** (1998). Cortical pathways to the mammalian amygdala. *Progress in Neurobiology*, 55, 257–332. [https://doi.org/10.1016/S0301-0082\(98\)00003-3](https://doi.org/10.1016/S0301-0082(98)00003-3)
- McNaughton, N.** (1989). *Biology and emotion*. Cambridge: Cambridge University Press.
- McNaughton, N.** (2019). Brain maps of fear and anxiety. *Nature Human Behaviour*, 3, 662–663. <https://doi.org/10.1038/s41562-019-0621-7>
- McNaughton, N.** (2020). Personality neuroscience and psychopathology: Should we start with biology and look for neural-level factors? *Personality Neuroscience*, 3, e4. <https://doi.org/10.1017/pen.2020.5>
- McNaughton, N., & Corr, P. J.** (2008). Animal cognition and human personality. In P. J. Corr (Ed.), *The reinforcement theory of personality* (pp. 95–119). Cambridge: Cambridge University Press.
- Miller, E. N., Hof, P. R., Sherwood, C. C., & Hopkins, W. D.** (2021). The paracingulate sulcus is a unique feature of the medial frontal cortex shared by great apes and humans. *Brain, Behavior and Evolution*, 96, 26–36. <https://doi.org/10.1159/000517293>
- Montag, C., Elhai, J., & Davis, K.** (2021). A comprehensive review of studies using the Affective Neuroscience personality scales in the psychological and psychiatric sciences. *Neuroscience & Biobehavioral Reviews*, 125, 160–167. <https://doi.org/10.1016/j.neubiorev.2021.02.019>
- Mota-Ortiz, S. R., Sukikara, M. H., Felicio, L. F., & Canteras, N. S.** (2009). Afferent connections to the rostralateral part of the periaqueductal gray: A critical region influencing the motivation drive to hunt and forage. *Neural Plasticity*, 2009, 1–11. <https://doi.org/10.1155/2009/612698>
- Murray, E. A.** (2007). The amygdala, reward and emotion. *Trends in Cognitive Sciences*, 11, 489–497. <https://doi.org/10.1016/j.tics.2007.08.013>
- O’Connell, L. A., & Hofmann, H. A.** (2012). Evolution of a vertebrate social decision-making network. *Science*, 336, 1154–1157. <https://doi.org/10.1126/science.1218889>
- Okon-Singer, H., Mehnert, J., Hoyer, J., Hellrung, L., Schaare, H. L., Dukart, J., & Villringer, A.** (2014). Neural control of vascular reactions: Impact of emotion and attention. *The Journal of Neuroscience*, 34, 4251–4259. <https://doi.org/10.1523/jneurosci.0747-13.2014>
- Perna, G., Vanni, G., Di Chiaro, N. V., Cavedini, P., & Caldirola, D.** (2014). Childhood trauma, temperament, and character in subjects with major depressive disorder and bipolar disorder. *The Journal of Nervous and Mental Disease*, 202, 695–698. <https://doi.org/10.1097/nmd.000000000000186>
- Perusini, J. N., & Fanselow, M. S.** (2015). Neurobehavioral perspectives on the distinction between fear and anxiety. *Learning & Memory*, 22, 417–425. <https://doi.org/10.1101/lm.039180.115>
- Pessoa, L., Padmala, S., Kenzer, A., & Bauer, A.** (2012). Interactions between cognition and emotion during response inhibition. *Emotion*, 12, 192–197. <https://doi.org/10.1037/a0024109>
- Piccinelli, M., Pini, S., Bellantuono, C., & Wilkinson, G.** (1995). Efficacy of drug treatment in obsessive-compulsive disorder: A meta-analytic review. *British Journal of Psychiatry*, 166, 424–443. <https://doi.org/10.1192/bjp.166.4.424>
- Pittendrigh, C. S.** (1958). Adaptation, natural selection and behaviour. In A. Roes & G. G. Simpson (Eds.), *Behaviour and evolution* (Vol. 1, pp. 390–416). New Haven: Yale University Press.
- Pollok, T. M., Kaiser, A., Kraaijenvanger, E. J., Monninger, M., Brandeis, D., Banaschewski, T., . . . Holz, N. E.** (2022). Neurostructural traces of early life adversities: A meta-analysis exploring age- and adversity-specific effects. *Neuroscience & Biobehavioral Reviews*, 135, 104589. <https://doi.org/10.1016/j.neubiorev.2022.104589>
- Qin, X., Liu, X.-X., Wang, Y., Wang, D., Song, Y., Zou, J.-X., . . . Zhang, W.-H.** (2021). Early life stress induces anxiety-like behavior during adulthood through dysregulation of neuronal plasticity in the basolateral amygdala. *Life Sciences*, 285, 119959. <https://doi.org/10.1016/j.lfs.2021.119959>
- Rademaker, A. R., Vermetten, E., Geuze, E., Mulwijik, A., & Kleber, R. J.** (2008). Self-reported early trauma as a predictor of adult personality: A study in a military sample. *Journal of Clinical Psychology*, 64, 863–875. <https://doi.org/10.1002/jclp.20495>
- Réus, G. Z., Abitante, M. S., Manosso, L. M., de Moura, A. B., Borba, L. A., Botelho, M. E. M., . . . Quevedo, J.** (2021). Environmental enrichment rescues oxidative stress and behavioral impairments induced by maternal care deprivation: Sex- and developmental-dependent differences. *Molecular Neurobiology*, 392, 2299. <https://doi.org/10.1007/s12035-021-02588-3>
- Revelle, W.** (2007). Experimental approaches to the study of personality. In B. Robins, R. C. Fraley & R. F. Krueger (Eds.), *Handbook of research methods in personality psychology* (pp. 37–61). New York: Guilford Press.
- Roberts, B. W., & DelVecchio, W. F.** (2000). The rank-order consistency of personality traits from childhood to old age: A quantitative review of longitudinal studies. *Psychological Bulletin*, 126, 3–25. <https://doi.org/10.1037/0033-2909.126.1.3>
- Roesch, M. R., & Olson, C. R.** (2004). Neuronal activity related to reward value and motivation in primate frontal cortex. *Science*, 304, 307–310. <https://doi.org/10.1126/science.1093223>
- Rolls, E. T.** (2017). The roles of the orbitofrontal cortex via the habenula in non-reward and depression, and in the responses of serotonin and dopamine neurons. *Neuroscience & Biobehavioral Reviews*, 75, 331–334. <https://doi.org/10.1016/j.neubiorev.2017.02.013>

- Russell, V., Allie, S., & Wiggins, T. (2000). Increased noradrenergic activity in prefrontal cortex slices of an animal model for attention-deficit hyperactivity disorder—the spontaneously hypertensive rat. *Behavioural Brain Research*, 117, 69–74. [https://doi.org/10.1016/S0166-4328\(00\)00291-6](https://doi.org/10.1016/S0166-4328(00)00291-6)
- Sable, H. J. K., Lester, D. B., Potter, J. L., Nolen, H. G., Cruthird, D. M., Estes, L. M., . . . Vorhees, C. V. (2021). An assessment of executive function in two different rat models of attention-deficit hyperactivity disorder: Spontaneously hypertensive versus Lphn3 knockout rats. *Genes, Brain and Behavior*, 20, e12767. <https://doi.org/10.1111/gbb.12767>
- Sadeghi, S., McIntosh, J., Shadli, S. M., Healey, D., Rostami, R., Trani, P., & McNaughton, N. (2018). Does behavioural inhibition system dysfunction contribute to Attention Deficit Hyperactivity Disorder? *Personality Neuroscience*, 2, e5. <https://doi.org/10.1017/pen.2019.5>
- Schouw, J. E. M. C., Verkes, R. J., Schene, A. H., & Schellekens, A. F. A. (2020). The relationship between childhood adversity and adult personality revealed by network analysis. *Child Abuse & Neglect*, 99, 104254. <https://doi.org/10.1016/j.chiabu.2019.104254>
- Schreiner, L., & Kling, A. (1953). Behavioral changes following rhinencephalic injury in cat. *Journal of Neurophysiology*, 16, 643–659. <https://doi.org/10.1152/jn.1953.16.6.643>
- Schuyler, B. S., Kral, T. R., Jacquart, J., Burghy, C. A., Weng, H. Y., Perlman, D. M., . . . Davidson, R. J. (2014). Temporal dynamics of emotional responding: Amygdala recovery predicts emotional traits. *Social Cognitive and Affective Neuroscience*, 9, 176–181. <https://doi.org/10.1093/scan/nss131>
- Sellbom, M. (2019). The MMPI-2-Restructured Form (MMPI-2-RF): Assessment of personality and psychopathology in the twenty-first century. *Annual Review of Clinical Psychology*, 15, 149–177. <https://doi.org/10.1146/annurev-clinpsy-050718-095701>
- Sequeira, S. L., Forbes, E. E., Hanson, J. L., & Silk, J. S. (2022). Positive valence systems in youth anxiety development: A scoping review. *Journal of Anxiety Disorders*, 89, 102588. <https://doi.org/10.1016/j.janxdis.2022.102588>
- Shackman, A. J., Salomons, T. V., Slagter, H. A., Fox, A. S., Winter, J. J., & Davidson, R. J. (2011). The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nature Reviews Neuroscience*, 12, 154–167. <https://doi.org/10.1038/nrn2994>
- Shadli, S. M., Ando, L. C., McIntosh, J., Lodhia, V., Russell, B. R., Kirk, I. J., . . . McNaughton, N. (2021). Right frontal anxiety-sensitive EEG ‘theta’ rhythm in the stop-signal task is a theory-based anxiety disorder biomarker. *Scientific Reports*, 11, 19746. <https://doi.org/10.1038/s41598-021-99374-x>
- Shadli, S. M., Glue, P., McIntosh, J., & McNaughton, N. (2015). An improved human anxiety process biomarker: Characterization of frequency band, personality and pharmacology. *Translational Psychiatry*, 5, e699. <https://doi.org/10.1038/tp.2015.188>
- Shadli, S. M., High, O., Byers, B., Gibbs, P., Steller, R., Glue, P., & McNaughton, N. (2020). Human anxiety-specific “theta” occurs with selective stopping and localizes to right inferior frontal gyrus. *Behavioral Neuroscience*, 134, 547–555. <https://doi.org/10.1037/bne0000316>
- Silva, C., & McNaughton, N. (2019). Are periaqueductal gray and dorsal raphe the foundation of appetitive and aversive control? A comprehensive review. *Progress in Neurobiology*, 177, 33–72. <https://doi.org/10.1016/j.pneurobio.2019.02.001>
- Smith, D. M., & Torregrossa, M. M. (2021). Valence encoding in the amygdala influences motivated behavior. *Behavioural Brain Research*, 411, 113370. <https://doi.org/10.1016/j.bbr.2021.113370>
- Snyder, P. J., Kaufman, R., Harrison, J., & Maruff, P. (2010). Charles Darwin’s emotional expression, experiment, and his contribution to modern neuropharmacology. *Journal of the History of the Neurosciences*, 19, 158–170. <https://doi.org/10.1080/09647040903506679>
- Soares, M. C., Gerlai, R., & Maximino, C. (2018). The integration of sociality, monoamines and stress neuroendocrinology in fish models: Applications in the neurosciences. *Journal of Fish Biology*, 93, 170–191. <https://doi.org/10.1111/jfb.13757>
- Stefanacci, L., & Amaral, D. G. (2002). Some observations on cortical inputs to the macaque monkey amygdala: An anterograde tracing study. *Journal of Comparative Neurology*, 451, 301–323. <https://doi.org/10.1002/cne.10339>
- Stephan, H., & Andy, O. J. (1969). Quantitative comparative neuroanatomy of primates: An attempt at a phylogenetic interpretation. *Annals of the New York Academy of Sciences*, 167, 370–387. <https://doi.org/10.1111/j.1749-6632.1969.tb20457.x>
- Sutherland, K. R., Alsop, B., McNaughton, N., Hyland, B. I., Tripp, G., & Wickens, J. R. (2009). Sensitivity to delay of reinforcement in two animal models of attention deficit hyperactivity disorder (ADHD). *Behavioural Brain Research*, 205, 372–376. <https://doi.org/10.1016/j.bbr.2009.07.011>
- Truini, A., Tinelli, E., Gerardi, M. C., Calistri, V., Iannuccelli, C., La Cesa, S., . . . Di Franco, M. (2016). Abnormal resting state functional connectivity of the periaqueductal grey in patients with fibromyalgia. *Clinical and Experimental Rheumatology*, 34, S129–133.
- Turton, R., Chami, R., & Treasure, J. (2017). Emotional eating, binge eating and animal models of binge-type eating disorders. *Current Obesity Reports*, 6, 217–228. <https://doi.org/10.1007/s13679-017-0265-8>
- van Ast, V. A., Spicer, J., Smith, E. E., Schmer-Galunder, S., Liberzon, I., Abelson, J. L., & Wager, T. D. (2016). Brain mechanisms of social threat effects on working memory. *Cerebral Cortex*, 26, 544–556. <https://doi.org/10.1093/cercor/bhu206>
- Varghese, M., Keshav, N., Jacot-Descombes, S., Warda, T., Wicinski, B., Dickstein, D. L., . . . Hof, P. R. (2017). Autism spectrum disorder: Neuropathology and animal models. *Acta Neuropathologica*, 134, 537–566. <https://doi.org/10.1007/s00401-017-1736-4>
- Verbruggen, F., Aron, A. R., Band, G. P., Beste, C., Bissett, P. G., Brockett, A. T., . . . Boehler, C. N. (2019). A consensus guide to capturing the ability to inhibit actions and impulsive behaviors in the stop-signal task. *eLife*, 8, e46323. <https://doi.org/10.7554/eLife.46323>
- Weimar, H. V., Wright, H. R., Warrick, C. R., Brown, A. M., Lugo, J. M., Freels, T. G., & McLaughlin, R. J. (2020). Long-term effects of maternal cannabis vapor exposure on emotional reactivity, social behavior, and behavioral flexibility in offspring. *Neuropharmacology*, 179, 108288. <https://doi.org/10.1016/j.neuropharm.2020.108288>
- Widiger, T. A. (2011). Personality and psychopathology. *World Psychiatry*, 10, 103–106. <https://doi.org/https://doi.org/10.1002/j.2051-5545.2011.tb00024.x>
- Wilson, G. D., Barrett, P. T., & Gray, J. A. (1989). Human reactions to reward and punishment: A questionnaire examination of Gray’s personality theory. *British Journal of Psychology*, 80, 509–515. <https://doi.org/10.1111/j.2044-8295.1989.tb02339.x>
- Wilson, G. D., Gray, J. A., & Barrett, P. T. (1990). A factor analysis of the Gray-Wilson personality questionnaire. *Personality and Individual Differences*, 11, 1037–1045. [https://doi.org/10.1016/0191-8869\(90\)90131-A](https://doi.org/10.1016/0191-8869(90)90131-A)
- Wilson, V., Weiss, A., Lefevre, C. E., Ochiai, T., Matsuzawa, T., Inoue-Murayama, M., . . . Altschul, D. (2020). Facial width-to-height ratio in chimpanzees: Links to age, sex and personality. *Evolution and Human Behavior*, 41, 226–234. <https://doi.org/10.1016/j.evolhumbehav.2020.03.001>
- Winship, I. R., Dursun, S. M., Baker, G. B., Balista, P. A., Kandratavicius, L., Maia-de-Oliveira, J. P., . . . Howland, J. G. (2018). An overview of animal models related to schizophrenia. *The Canadian Journal of Psychiatry*, 64, 5–17. <https://doi.org/10.1177/0706743718773728>
- Yamaguchi, T., Danjo, T., Pastan, I., Hikida, T., & Nakanishi, S. (2013). Distinct roles of segregated transmission of the septo-habenular pathway in anxiety and fear. *Neuron*, 78, 537–544. <https://doi.org/10.1016/j.neuron.2013.02.035>
- Yee, D. M., Leng, X., Shenav, A., & Braver, T. S. (2022). Aversive motivation and cognitive control. *Neuroscience & Biobehavioral Reviews*, 133, 104493. <https://doi.org/10.1016/j.neubiorev.2021.12.016>
- Zanta, N. C., Suchecki, D., & Girardi, C. E. N. (2021). Early life stress alters emotional learning in a sex- and age-dependent manner with no impact on emotional behaviors. *Developmental Psychobiology*, 63, e22182. <https://doi.org/10.1002/dev.22182>