

Author's Response

The Conceptualisation, Measurement and Scope of Reinforcement Sensitivity in the Context of a Neuroscience of Personality

LUKE D. SMILLIE*

Department of Psychology, Goldsmiths, University of London, UK

Abstract

Reinforcement sensitivity theory (RST) is complex, and there are subtle differences between RST and other approach-avoidance process theories of personality. However, most such theories posit a common biobehavioural mechanism underlying personality which we must therefore strive to understand: differential sensitivity to reinforcing stimuli. Reinforcement sensitivity is widely assessed using questionnaires, but should we treat such measures as (a) a proxy for reinforcement sensitivity itself (i.e. the underlying causes of personality) or (b) trait constructs potentially manifesting out of reinforcement sensitivity (i.e. the 'surface' of personality)? Might neuroscience paradigms, such as those I have reviewed in my target paper, provide an advantage over questionnaires in allowing us to move closer to (a), thereby improving both the measurement and our understanding of reinforcement sensitivity? Assuming we can achieve this, how useful is reinforcement sensitivity—and biological perspectives more generally—for explaining personality? These are the major questions raised in the discussion of my target paper, and among the most pertinent issues in this field today. Copyright © 2008 John Wiley & Sons, Ltd.

It was a great pleasure to read the energetic and engaging commentary which my target paper has received. I am especially honoured to receive thoughtful critique from some of the most well-respected figures working with reinforcement sensitivity theory specifically (RST) (**Avila & Torrubia; Chavanon, Stemmler & Wacker; Corr; McNaughton; Reuter & Montag**), related approach-avoidance process theories (**Carver; Cloninger**), and personality psychology more generally (**Johnson & Deary; Matthews; Revelle &**

*Correspondence to: Luke D. Smillie, Department of Psychology, Goldsmiths, University of London, London, SE14 6NW, UK. E-mail: l.smillie@gold.ac.uk

Wilt). Some of the above are experts in the specific neuroscience methods discussed in my target paper, the conclusions of which are qualified by their sage counsel.

The primary aim of my paper was to consider the question ‘What is reinforcement sensitivity?’ The problem is both methodological (i.e. how should we measure reinforcement sensitivity?) and conceptual (i.e. how do we conceptualise reinforcement sensitivity?). On balance, most commentators shared my enthusiasm for neuroscience paradigms as a means to help answer this question (especially **Chavanon, Stemmler & Wacker; Cloninger; McNaughton; Reuter & Montag**). Most, however, also cautioned against biological fundamentalism (especially **Carver; Matthews; Revelle & Wilt**), and some objected to my dismissal of questionnaire-based measurement of reinforcement sensitivity (especially **Avila & Torribia; Corr**). Probing points were also made in relation to the relative scope of RST, and other biologically driven theories, as explanations of personality (especially **Carver; Cloninger; Johnson & Deary; Matthews; Revelle & Wilt**).

In my rejoinder, I consider the major themes which have emerged from the discussion. First, I begin with some brief theoretical clarifications. Second, I discuss the usefulness (or lack thereof) of self-report measures of reinforcement sensitivity. Third, I consider the challenges which have been highlighted in relation to neuroscience paradigms as a means to assess reinforcement sensitivity. Finally, I consider the restricted role that reinforcement sensitivity is likely to have in explaining personality variation.

THEORETICAL CLARIFICATIONS

My target paper has focussed on one issue within a broad context at the expense of due consideration of the context. As **Avila and Torribia** note, my discussion of background details was somewhat compressed. Given the numerous existing reviews which describe the theory and history of RST (e.g. Corr, 2004, 2008; Matthews & Gilliland, 1999; Pickering & Gray, 2001), I wished to avoid redundancy and repetition. As a consequence, however, important issues in RST and related approach-avoidance process theories were perhaps insufficiently emphasised (e.g. as noted by **McNaughton**).

A general point to concede is the limited extent to which one can generalise from RST to the broader family of approach-avoidance process theories of personality. That these theories are not all interchangeable was demonstrated by the fact that, in their commentaries, both **Carver** and **Cloninger** (whose work I identified as part of this family) drew strong distinctions between their own perspectives and that provided by RST. Despite their unique features, however, both of these models incorporate reinforcement sensitivity mechanisms which are directly modelled on RST. **Chavanon, Stemmler and Wacker** illustrate this point by framing RST as a sub-theory of personality processes; personality may have a motivational component, and part of that component is dealt with by RST. Thus, despite the subtleties and complexities of approach-avoidance process theories of personality, the question of reinforcement sensitivity *per se* seems fundamental.

‘Reinforcement sensitivity’ is importantly distinct from ‘reinforcement’ (**Avila & Torribia; Corr** and **McNaughton**). Some of the paradigms I have discussed may be better suited to study of the latter, but only the former is of central interest for us. For instance, **McNaughton** makes the pertinent point that some pharmacological manipulations modulate the sensitivity of approach and avoidance systems, while others simply activate them. Similarly, **Avila and Torribia** note that someone’s experimentally measured reinforcement sensitivity must be separated from their subjective value of the reinforcer

(see also **Revelle & Wilt's** windsurfing analogy). Such distinctions resonate with the insight provided by computational models (e.g. Cohen, 2007; Pesola & Pickering, 2006). Pesola and Pickering found that a model incorporating variation in the DA input weight (simulating differences in the effect of reward on reward circuitry) provides a less adequate fit to personality related differences in behavioural data than does a model which varies the DA output weight (simulating differences in *reward prediction error*; the known output of DA neurons; Schultz, 1998, 2007). Appreciating such distinctions seems crucial if we are not to be sidetracked in our attempts to operationalise the causal mechanisms of approach-avoidance process theories.

In addition to reward and punishment sensitivity, since the revision of RST (Gray & McNaughton, 2000), we must contend with the more complex and confusable concept of conflict sensitivity. **Carver** wonders how approach-approach or avoidance-avoidance conflicts can occur, given that the BIS is only engaged by joint activation of the FFFS and BAS (see Figure 2 of target paper). As my colleagues and I have previously suggested (Smillie, Pickering, & Jackson, 2006), incompatible approach goals appear to signal both incentive (gain of reward) and threat (loss of reward). (Shorthand terms such as 'threat' may lead us to forget that frustrative nonreward functions as a 'punisher', as noted by **Corr**.) As an archetypal everyday instance of approach-approach conflict, Chris Jackson (Personal Communication) uses the example of the 'agony of choice' we might experience when deciding between two chocolates in a lolly shop; we know that when we select one, we forfeit the other (**Chavanon, Stemmler & Wacker** use a similar example). Obviously, we do not experience intense anxiety in such situations, as we might when walking home (approach) requires crossing a deserted park notorious for muggings (avoid)—but this is surely because being mugged is more aversive to us than is missing out on a chocolate.

Reinforcement sensitivity is manifestly concerned with motivation and emotion (e.g. as represented in Figure 1 of the target paper), but it is not, as **Revelle and Wilt** suggest, unrelated to cognitive processes. For instance, RST assumes that the systems which mediate reinforcement direct attention and information processing resources toward the stimuli (Corr, Pickering, & Gray, 1997). Further, as emphasised by **McNaughton**, the functioning of the BIS cannot simply be reduced to threat sensitivity (a point also touched on by **Carver**), and its familiar role in anxiety is connected with its lesser emphasised role in memory. The BIS monitors goals and is engaged by conflict (i.e. mutually incompatible goals), at which point it increases the valence of affectively negative *stimuli* and *stored associations* until the conflict is resolved (i.e. until the more negatively valenced goal is suppressed). The direct consequence is behavioural inhibition (for the duration of the experienced conflict), while the indirect consequence is modification of relevant stored memories (for further details see Gray, 1985, and Gray & McNaughton, 2000, chapters 1, 8 and 9). RST provides a far from complete account of cognitive processes, but the functions of the systems are 'quintessentially cognitive in nature' (Gray, 1985, p. 110).

Least surprising in the context of a bottom-up model is disagreement among researchers as to the specific personality traits at which we will arrive from an analysis of reinforcement sensitivity. As **Carver** notes, Gray's (1981) original suggestion that the BIS and BAS may manifest as trait anxiety and impulsivity has faced its share of challenges—especially in the case of impulsivity (see Pickering & Gray, 2001; Pickering & Smillie, 2008; Smillie et al., 2006). **Avila and Torrubia** disagree with my linking of reward and punishment sensitivity broadly to Extraversion and Neuroticism; while I have cited evidence to support such a representation it is of course not unequivocal. Again, my view

is that until we successfully measure reinforcement sensitivity we cannot be certain of its relationship with personality.

CAN WE ASSESS THE CAUSES OF PERSONALITY WITH PERSONALITY QUESTIONNAIRES?

In my target paper I have asked the question ‘What is reinforcement sensitivity?’, and considered paradigms that may help us to answer it. I began by suggesting that psychometric paradigms (purpose-built RST questionnaires) might be ‘less-than-ideal for this purpose’. While some, such as **McNaughton and Reuter and Montag** concur with this point, others—particularly **Avila and Torrubia; Corr and Revelle and Wilt**—do not.

My position is that personality questionnaires are ideal for describing personality but are less suited to assessing the underlying biobehavioural causes of personality. Jackson (2003) refers to the ability of self-report questionnaires to capture the ‘surface’ of personality. That is, measures such as Extraversion or Neuroticism reflect aspects of our temperament which are observable ‘at the surface’ (e.g. to the respondent completing a self-report questionnaire measure). A similar yet more elaborated view is presented by **Revelle and Wilt**, who conceptualise personality as the long-term patterning of our affect, behaviour, cognition and desires (the ‘ABCDs’ of personality). Our understanding of personality is thus a descriptive summary; a ‘downstream manifestation of multiple interacting state processes’ (**Corr**), emerging ‘from multiple neurological and cognitive components’ (**Matthews**). Theories such as RST attempt to identify *some* of the biobehavioural processes ‘beneath the surface of’ or ‘up-stream from’ personality. In comparison with potential ‘surface-level’ or ‘downstream’ influences on personality (e.g. self efficacy), biobehavioural processes such as reinforcement sensitivity lie at a fundamentally different level of analysis.

Questionnaires such as the BIS/BAS scales (Carver & White, 1994), the Appetitive Motivation Scale (Cooper, Smillie & Jackson, in press), or the Sensitivity to Reward and Punishment Questionnaire (Torrubia, Avila, Molto, & Caseras, 2001) are narrow-focus, theoretically derived personality measures. They play a useful role in conceptualising potential trait manifestations of the BIS, BAS and FFFS which should not be forgotten in the wake of new methodologies (**Avila & Torrubia and Reuter & Montag**). How are these scales different from broad-focus, empirically derived personality measures such as Extraversion from the EPQ-R (H. J. Eysenck & S. B. G. Eysenck, 1992)? They certainly differ in terms of construct bandwidth, but can we say they differ in level of analysis? Can we say that one lies at the ‘surface’ of personality while another lies more closely to the underlying causes? Suggesting such is claiming that *some* questionnaires index downstream, conscious introspections (e.g., EPQ-R Neuroticism: ‘*Do you often worry about things you should not have done or said?*’) while others, somehow, are a hotline to upstream neural parameters (e.g., SPSRQ Sensitivity to Punishment: ‘*Are you often worried by things that you said or did?*’). We cannot have our cake and eat it too.¹

Corr suggests that we assess reinforcement sensitivity using ‘theoretically faithful measures of personality’ (e.g. BIS/BAS/FFFS scales), which we then correlate with both

¹**Avila and Torrubia** risk this position by accepting my argument as it applies to **Carver’s** questionnaire but rejecting it as it applies to their own.

“bottom-up” neural processes (e.g. dopamine and category learning) and “top-down” personality measures (e.g. Extraversion and Neuroticism). However, so-called ‘intermediate’ measures of personality are (presumably) ‘theoretically faithful’ only to the extent that they reflect the biobehavioural processes delineated *in the theory*. And yet, by committing to these questionnaires as our gold standard we are logically compelled to validate biobehavioural parameters against them, rather than the other way around. Would we accept the validity of a rationally designed trait measure of reward sensitivity if it had no relationship with dopamine function or behavioural reactions to reward? If the answer is no, then we are, at least implicitly, adopting a bottom-up approach which retains all elements of **Corr’s** recommendation but involves ‘switching the perspective’ (as advocated by **Reuter & Montag**). For instance, Haas, Omura, Constable, and Canli (2007) demonstrate that conflict-related amygdala activation predicts trait anxiety, which is in turn a subscale of Neuroticism. In this way, a bottom-up perspective to studying the relevance of reinforcement sensitivity to personality may allow us to zero-in on relevant traits (in terms of their relationship with multiple biobehavioural indices of reinforcement sensitivity) and situate those traits within the broader structure of personality.

While I consider that personality questionnaires are not the most suitable method for studying the causes of personality, I am not suggesting that they be subject to lower status (**Revelle & Wilt**).² ‘Feeling short of breath’ is a self-reportable subjective state, which is likely to correlate with broader self-report measures of health and well-being, and which may potentially be explained by an underlying biological condition such as pneumothorax (collapsed lung). We can use computed tomography (CT) to assess the state of the lungs, and potentially explain shortness of breath specifically and poor subjective well-being more generally. All three measures have useful information to offer, and no one would suggest that the subjective experience of shortness of breath is of ‘lesser status’ than an CT-scan of the chest (except as potential *explanation* of poor health). In the same way, questionnaires are invaluable to personality psychologists, because they provide our measures of personality (**Avila & Torribia**). But as down-stream, surface-level summaries of our ABCDs, they are far removed from the biobehavioural variations proposed as partial explanations of personality (Wilson, Barrett & Gray, 1989, p. 84).

HOW USEFUL ARE NEUROSCIENCE METHODS FOR STUDYING (NEURAL) CAUSES OF PERSONALITY?

The view that questionnaires may not be ideal for the measurement and conceptualisation of reinforcement sensitivity does not allow neuroscience methods to win by default. The paradigms I reviewed appeared promising to me, and as a neuroscience novice I am encouraged by the broadly supportive comments which my target paper has received from experts in this area (especially **Chavanon, Stemmler & Wacker; McNaughton and Reuter & Montag**). Nevertheless, as noted in the conclusion of my target paper, and elaborated upon in the open peer commentary, there are challenges associated with these paradigms.

²**Revelle and Wilt** argue that biological and (both objectively and subjectively measured) behavioural data are equally valuable for indexing latent variables such as reinforcement sensitivity. In addition to my earlier points, I should note that behaviour (e.g. responses on a category-learning task) is not necessarily equivalent to *self-reports* of behaviour. Consider, for example, the typically low association between impulsivity questionnaire scores and (similarly conceptualised) actual impulsive behaviour (e.g., Reynolds, Ortengren, Richards, & de Wit, 2006).

Perhaps the greatest challenge is created by the fact that the brain is not a series of closed systems (see Pickering & Gray, 2001, p. 113). Although DA drives reward processing, it does not operate in a vacuum; 5HT and NA are known modulators of DA function and also have some involvement in reward processing (Cardinal, 2006). Similarly, depressive disorders are linked not only with 5HT and NA but also (perhaps with insufficient emphasis) reduced DA transmission (Montgomery, 2008). **Avila and Torrubia** provide a further example: The amygdala is not only a component of the BIS and FFFS but has an empirically demonstrable role in reward processing. Thus, we cannot simplistically state that amygdala activity = punishment sensitivity. No single biobehavioural parameter is likely to provide an isomorphic representation of reinforcement sensitivity (as **McNaughton** stresses, providing additional pertinent examples). To meet this challenge, we must (a) identify when and in what way a particular parameter is involved in reinforcement sensitivity (as, e.g. the Blanchards have done in the case of defensive behaviour; R. J. Blanchard, Griebel, Henrie, & D. C. Blanchard, 1997), and (b) investigate *multiple* parameters of reinforcement sensitivity simultaneously, in order to 'move beyond a series of disconnected demonstrations that there are linkages between personality, genes and brain systems' (**Matthews**).

While **McNaughton** suggests that these multiple, interacting parameters may emerge as a single latent factor, **Matthews** is more pessimistic. As he notes, the near-intractable Eysenckian construct of cortical arousal serves as a lesson that such a tidy state of affairs may not emerge (see Matthews & Gilliland, 1999). To my knowledge, no one has determined, for example whether or not genetic and neural indices of reward sensitivity form a single latent variable in a structural equation model. We might take some encouragement from the fact that such indices have concerted relationships with traits and behaviour (e.g. Dalley et al.'s, 2007, behavioural model of reward reactivity simultaneously captured multiple sources of relevant behavioural and neural variation). Over and above this, we should perhaps be open to the possibility of multi-faceted models of reinforcement sensitivity (*cf.* Gray and McNaughton's, 2000, fractioning of the defence system originally described by Gray, 1982).

As **Cloninger**, **Mathews** and **Reuter and Montag** note, relationships between neural activity and personality scores are likely to be complex and nonlinear, creating difficulties when mapping biobehavioural reinforcement sensitivity parameters to personality traits. For instance, Pesola and Pickering (2006) found that EPQ-Extraversion (along with other BAS-related trait measures) was negatively associated with a reward-related learning parameter during category learning. While this result seems opposite to the rational prediction one might make from RST, the data were successfully modelled using a reward prediction error (RPE) representation of BAS variation. It seemed that large RPE errors (i.e., a strong response to an unpredicted reward, representing high-BAS) result in subsequent reward predictions which are too high, which means that subsequent rewards are *smaller* than predicted (and therefore RPE-driven learning is lessened). Thus, according to the model, learning initially increases as a function of RPE but then steadily decreases (plausibly explaining why, in Pesola and Pickering's behavioural data, low extraversion was a stronger predictor of learning than was high extraversion). This example demonstrates the powerful role which formal and computational models may play in meeting arising challenges, such as nonlinear effects (**Cloninger**) and nuisance variables (**Carver**), when attempting to map neural parameters to personality traits (**Matthews**) (as emphasised by Pickering, 2008).

An additional, sobering point is made by **Reuter and Montag** regarding the formidable economic and skill requirements of neuroscience methods. Although this is a logistical problem, and entirely independent of questions regarding the validity of paradigms such as those I have reviewed, it is relevant to the effectiveness of my target paper as an instrument for change. There are also ethical concerns which may preclude the use of many paradigms for human research in many of our laboratories such as benzodiazepine drug manipulations discussed by **McNaughton**. This does not, however, prevent us from collaborating with colleagues who possess the skills and resources that we ourselves may lack (as noted by **Reuter & Montag**) and ensuring that our own non-biological work is biologically plausible (a priority underlined by **Revelle & Wilt**). If we do not attempt to address the challenges posed by neuroscientific methods we are, in effect, suggesting that the biological bases of personality are not worth the effort to understand.

WHAT IS THE SCOPE OF REINFORCEMENT SENSITIVITY AS A MODEL FOR PERSONALITY?

Reinforcement sensitivity will almost certainly fail to provide a sufficient explanation of personality even if it does provide a necessary one (as has always been explicitly asserted, e.g. Gray, 1973, p. 415). This is the common issue raised by **Carver; Cloninger; Johnson and Deary; Matthews and Revelle and Wilt**. Biobehavioural processes offer, at best, a partial explanation of personality (**Cloninger**), and many aspects of personality might be most powerfully explained in terms of social and cognitive processes (**Matthews**). However, this does not mean that the partial explanation of personality which RST may provide is unimportant. Nor, incidentally, should we imagine that social and cognitive processes are not produced or mediated by brain structures and functions, including those connected with reinforcement sensitivity.

Efforts to understand the heritable, biological bases of personality are often mistaken for the view that personality can be entirely reduced to one heritable, biological model (e.g. consider the title chosen by **Revelle and Wilt** for their commentary). Given that only 50% of the variance in personality can be attributed to genetic factors (Bouchard, Lykken, Segal, & Tellegen, 1990), coupled with the fact that that reinforcement sensitivity seems unlikely to capture all heritable, biological antecedents of personality (e.g. see **Cloninger**), theories such as RST are clearly potential explanations of a small fraction of personality variance. However, finite scope is not an ultimate limitation, as **Johnson and Deary** appear to suggest with the analogy that RST might be 'the Newtonian Mechanics of personality'. Ironically, suggesting that it explains personality as successfully as Newtonian Mechanics explains motion and gravity seems to overstate the validity of RST. In any case, the analogy as intended seems a little premature given that there is no 'general relativity theory of personality' available to displace RST (yet!).

Many 'alternative' perspectives to RST (e.g. those provided by **Carver and Cloninger**) are not paradigm shifts. Rather, they are extensions of RST which often explicitly assume reinforcement sensitivity at one level of explanation. **Cloninger** has developed what is almost certainly the most well-known extension to RST. His model distinguishes between lower-level 'temperament' dimensions, which represent those aspects of personality which are largely determined by reinforcement sensitivity (and other biological dispositions), and upper-level 'character' dimensions, which represent those aspects of personality which are not determined by reinforcement sensitivity (notably, those reflecting the

influence of maturation and the environment). Consistent with my view that we cannot use questionnaires to measure different levels of analysis (e.g. 'biological' and 'non-biological' aspects of personality), both the Temperament and Character dimensions in **Cloninger's** model have been shown to have significant genetic components (e.g. Ando et al., 2004). Nevertheless, I agree that multiple levels of explanation for personality must be sought, and that reinforcement sensitivity cannot cover all bases.

Carver also presents a two-level model, in which approach and avoidance processes are again represented at a lower 'reflexive' level, while the upper 'reflective' level represents executive control over these processes. Such gate-keeping seems not only plausible, but essential; we consciously interrupt our approach and avoidance processes every day for reasons which may or may not (directly) concern reinforcement. RST might not (presently) offer an explanation for this, and the model presented by **Carver** is one suggestion for how it might be extended.³ Interestingly, this model suggests a possible explanation of the behaviour discussed by **Johnson and Deary** to demonstrate the finite reach of RST. Specifically, they cite both animal and human data which provide evidence of individual differences in tolerance (and even approach) of punishment in order to secure long-term reward. Perhaps, this can be explained by the moderating action of reflective executive control over reinforcement sensitivity. (A related example is provided by **Revelle & Wilt**, using a three-level framework outlined by Ortony et al., 2005, which is very similar to the approach favoured by **Carver**). It is indeed important to realise the scope of RST, with examples such as these reminding us that it does not provide a full account of personality. At the same time, one should not confuse a theory's scope with its validity; the potential role of executive processes in personality does not undermine the potential role of approach-avoidance processes.⁴

Some cognitive and social/environmental perspectives come closer to *modifying* (as opposed to *extending*) approach-avoidance process theories. Both here and elsewhere (Matthews & Gilliland, 1999; Matthews, 2008a,b), **Matthews** blocks the one-way road to biological fundamentalism. Specifically, he demonstrates the influence of cognitive processes on behaviours which theories, such as RST, explain only in terms of biological processes. An example is the moderating role of expectancies in the effects of drugs on behaviour (related points are made by **Avila and Torribia** and **Revelle and Wilt**). While I agree with **Matthews** that the study of cognitive parameters can reveal limitations to biological explanation, the biological-cognitive distinction itself is a false dichotomy; cognitive processes such as expectancies are not separate from processes in the brain. Recall that DA neurons do not simply communicate that a reward has occurred but, more specifically, that a reward has occurred which is greater (or lesser) than was *expected* (Schultz, 1998, 2007). Our earlier understanding of reward sensitivity may not have accounted for this, but it clearly should (see Pickering & Smillie, 2008). In this case, modification of our understanding of biobehavioural reward sensitivity has been driven by

³**Carver** suggests that the BIS may underlie the reflective executive system, and perhaps relate to trait conscientiousness via the process of executive control (rather than to trait anxiety/neuroticism via the process of avoidance/inhibition). As the functional neurobiology of the BIS is the septo-hippocampal system (e.g. Gray & McNaughton, 2000), while executive processes are primarily localised to the lateral prefrontal cortex (e.g. Tanji & Hoshi, 2008), this proposal might not be wholly biologically plausible. Psychological theory needs to be viewed through the lens of biological phenomena (**Cloninger**), and *vice versa* (**Carver**).

⁴The reverse is of course also true. For example, heritable individual differences in reinforcement sensitivity demonstrated by cross-fostering studies (see Gray, 1987, chapter 4) do not negate a role for the maternal treatment of rat pups (the focus of some of the research summarised by **Johnson & Deary**).

biological data, although it might just as well have been driven by the cognitive challenges presented by **Matthews**.

Chavanon, Stemmler and Wacker argue for an integrated cognitive neuroscience approach to personality explanation, emphasising the relevance of reinforcement sensitivity to cognitive processes and of cognitive processes to approach and avoidance processes. They identify the relevance of cognitive paradigms such as decision-making tasks and cortical parameters such as EEG asymmetry. **Chavanon, Stemmler and Wacker** have presented an EEG model consisting of cortical signatures of reinforcement sensitivity, whereby left anterior activation reflects BAS or FFFS function, while right anterior activation reflects conflict-induced BIS activation (see Wacker et al., 2003, 2008). Such a model might be well-placed to account for cognitive processes typically linked with cortical function (e.g. Tanji & Hoshi, 2008); indeed, this has been demonstrated in the case of contextual effects on avoidance processes (see Crost, Pauls & Wacker, 2008). It is not difficult to imagine such a model and data being presented in criticism of RST but, in fact, what **Chavanon, Stemmler and Wacker** strive for is an extension of the model as it is traditionally represented, such that it might provide a more complete account of the cognitive processes which are relevant to approach and avoidance (e.g. 'structuring and restructuring cognitive networks in line with goals, means and situational affordances').

In exploring neuroscience paradigms for approach-avoidance process theories of personality, we should not expect that they will provide complete explanations of personality. However, we should not confuse the scope of a theory with its limitations. Further, the challenges identified by cognitive and social psychology (as noted by **Matthews** and **Revelle & Wilt**) should not lead us to form false dichotomies. Indeed, these challenges may often suggest a way for the theory to move forward.

REFERENCES TO DISCUSSION SECTION

- Ando, J., Suzuki, A., Yamagata, S., Kijima, N., Maekawa, H., Ono, Y., et al. (2004). Genetic and environmental structure of Cloninger's temperament and character dimensions. *Journal of Personality Disorders*, *18*, 379–393.
- Atkinson, J. W. (1957). Motivational determinants of risk-taking behavior. *Psychological Review*, *64*, 359–372.
- Atkinson, J. W. (1974). Strength of motivation and efficiency of performance. In J. W. Atkinson, & J. O. Raynor (Eds.), *Motivation and achievement* (pp. 117–142). New York: Winston (Halsted Press/Wiley).
- Averill, J. R. (1997). The emotions: An integrative approach. In R. Hogan, J. A. Johnson, & S. R. Briggs (Eds.), *Handbook of personality psychology* (pp. 513–541). San Diego, CA: Academic Press.
- Ávila, C., & Torrubia, R. (2008). Performance and conditioning studies. In P. J. Corr (Ed.), *The reinforcement sensitivity theory of personality*. Cambridge, UK: Cambridge University Press.
- Becerra, L., & Borsook, D. (in press). Signal valence in the nucleus accumbens to pain onset and offset. *European Journal of Pain*. DOI: 10.1016/j.ejpain.2007.12.007
- Blanchard, R. J., & Blanchard, D. C. (1990a). Anti-predator defense as models of animal fear and anxiety. In P. F. Brain, S. Parmigiani, R. J. Blanchard, & D. Mainardi (Eds.), *Fear and defence* (pp. 89–108). Chur, Switzerland: Harwood Academic Publishers.
- Blanchard, R. J., & Blanchard, D. C. (1990b). An ethoexperimental analysis of defense, fear and anxiety. In N. McNaughton, & G. Andrews (Eds.), *Anxiety* (pp. 124–133). Dunedin, NZ: Otago University Press.

- Blanchard, R. J., Griebel, G., Henrie, J. A., & Blanchard, D. C. (1997). Differentiation of anxiolytic and panicolytic drugs by effects on rat and mouse defense test batteries. *Neuroscience and Biobehavioural Reviews*, *21*, 783–789.
- Born, W. K., Revelle, W., & Pinto, L. H. (2002). Improving biology performance with workshop groups. *Journal of Science Education and Technology*, *11*, 347–365.
- Bouchard, T. J., Lykken, M. M., Segal, N. L., & Tellegen, A. (1990). Sources of human psychological differences: The Minnesota study of twins reared apart. *Science*, *250*, 223–228.
- Broadbent, D. (1971). *Decision and stress*. London, UK: Academic Press.
- Broadhurst, P. L. (1957). Emotionality and the Yerkes-Dodson law. *Journal of Experimental Psychology*, *54*, 345–351.
- Cardinal, R. N. (2006). Neural systems implicated in delayed and probabilistic reinforcement. *Neural Networks*, *19*, 1277–1301.
- Carver, C. S. (2005). Impulse and constraint: Perspectives from personality psychology, convergence with theory in other areas, and potential for integration. *Personality and Social Psychology Review*, *9*, 312–333.
- Carver, C. S., Johnson, S. L., & Joormann, J. (2008). *Two-mode models of self-regulation: Interpreting the role of low serotonergic function in vulnerability to depression*. Submitted for publication.
- Carver, C. S., & Miller, C. J. (2006). Relations of serotonin function to personality: Current views and a key methodological issue. *Psychiatry Research*, *144*, 1–15.
- Carver, C. S., & Scheier, M. F. (1982). Control theory: A useful conceptual framework for personality-social, clinical, and health psychology. *Psychological Bulletin*, *92*, 111–135.
- Caspi, A., & Shiner, R. L. (2006). Personality development. In W. Damon, & R. Lerner (Series Eds.) & N. Eisenberg (Vol. Ed.), *Handbook of child psychology*, Vol. 3. *Social, emotional, and personality development* (6th ed., pp. 300–365). New York, NY: Wiley.
- Carver, C. S., & White, T. L. (1994). Behavioural inhibition, behavioural activation, and affective responses to impending reward and punishment: The BIS/BAS scales. *Journal of Personality and Social Psychology*, *67*, 319–333.
- Cavigelli, S. A., & McClintock, M. K. (2003). Fear of novelty in infant rats predicts corticosterone dynamics and an early death. *Proceedings of the National Academy of Sciences USA*, *100*, 16131–16136.
- Chavanon, M.-L., Wacker, J., Leue, A., & Stemmler, G. (2007). Frontal asymmetry during approach-avoidance conflict. In J. Hennig, M. Reuter, C. Montag, & P. Netter (Eds.), *Abstracts of the 13th Biennial Meeting of the International Society for the Study of Individual Differences (ISSID)* (pp. 67–68). Göttingen, Germany: Hogrefe & Huber Publishers.
- Chomsky, N. (1980). Rules and representations. *Behavioral and Brain Sciences*, *3*, 1–61.
- Cloninger, C. R. (1987). A systematic method for clinical description and classification of personality variants: A proposal. *Archives of General Psychiatry*, *44*, 573–587.
- Cloninger, C. R. (2004). *Feeling good: The science of well being*. New York, NY: Oxford University Press.
- Cloninger, C. R., Svrakic, D. M., & Przybeck, T. R. (1993). A psychobiological model of temperament and character. *Archives of General Psychiatry*, *50*, 975–990.
- Coan, J. A., & Allen, J. J. B. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology*, *67*, 7–49.
- Cohen, M. X. (2007). Individual differences and the neural representations of reward expectation and reward prediction error. *Social Cognitive and Affective Neuroscience*, *2*, 20–30.
- Cooper, A., Smillie, L. D., & Jackson, C. J. (in press). A trait conceptualisation of reward-reactivity: Psychometric properties of the Appetitive Motivation Scale (AMS). *Journal of Individual Differences*.
- Corr, P. J. (2002a). J. A. Gray's reinforcement sensitivity theory and frustrative nonreward: A theoretical note on expectancies in reactions to rewarding stimuli. *Personality and Individual Differences*, *32*, 1247–1253.
- Corr, P. J. (2002b). J. A. Gray's reinforcement sensitivity theory: Tests of the joint subsystems hypothesis of anxiety and impulsivity. *Personality and Individual Differences*, *33*, 511–532.
- Corr, P. J. (2004). Reinforcement sensitivity theory and personality. *Neuroscience and Biobehavioral Reviews*, *28*, 317–332.

- Corr, P. J. (Ed.). (2008). *The reinforcement sensitivity theory of personality*. Cambridge, UK: Cambridge University Press.
- Corr, P. J., Kumari, V., Wilson, G. D., Checkley, S., & Gray, J. A. (1997). Harm avoidance and affective modulation of the startle reflex: A replication. *Personality and Individual Differences*, 22, 591–593.
- Corr, P. J., Pickering, A. D., & Gray, J. A. (1997). Personality, punishment and procedural learning: A test of J.A. Gray's anxiety theory. *Journal of Personality and Social Psychology*, 73, 337–344.
- Corr, P. J., Wilson, G. D., Fotiadou, M., Kumari, V., Gray, N. S., Checkley, S., et al. (1995). Personality and affective modulation of the startle reflex. *Personality and Individual Differences*, 19, 543–553.
- Costa, P. T., & McCrae, R. R. (1992). Four ways five factors are basic. *Personality and Individual Differences*, 13, 653–665.
- Crost, N. W., Pauls, C. A., & Wacker, J. (2008). Defensiveness and anxiety predict frontal EEG asymmetry only in specific situational contexts. *Biological Psychology*, 78, 43–52.
- Dalley, J. W., Fryer, T. D., Brichard, L., Robinson, E. S., Theobald, D. E., Lane, K., et al. (2007). Nucleus accumbens D2/3 receptors predict trait impulsivity and cocaine reinforcement. *Science*, 315, 1267–1270.
- Davidson, R. J., Marshall, J. R., Tomarken, A. J., & Henriques, J. B. (2000). While a phobic waits: Regional brain electrical and autonomic activity in social phobics during anticipation of public speaking. *Biological Psychiatry*, 47, 85–95.
- Depue, R. A., & Lenzenweger, M. F. (2005). A neurobiological dimensional model of personality disturbance. In M. F., Lenzenweger, & J. F. Clarkin (Eds.), *Major theories of personality disorder* (2nd ed., pp. 391–453). New York, NY: Guilford Press.
- Depue, R. A., & Spont, M. R. (1986). Conceptualizing a serotonin trait: A behavioral dimension of constraint. *Annals of the New York Academy of Sciences*, 487, 47–62.
- Eisenberg, D. T. A., MacKillop, J. M., Modi, M., Beauchemin, J., Dang, D., Lisman, S., et al. (2007). Examining impulsivity as an endophenotype using a behavioral approach: A *DRD2 Taq1 A* and *DRD4 48-bp VNTR* association study. *Behavioral and Brain Functions*, 3:2.
- Eisenberg, N., Spinrad, T. L., Fabes, R. A., Reiser, M., Cumberland, A., Shepard, S. A., et al. (2004). The relations of effortful control and impulsivity to children's resiliency and adjustment. *Child Development*, 75, 25–46.
- Elliot, A. J., & Church, M. A. (1997). A hierarchical model of approach and avoidance achievement motivation. *Journal of Personality and Social Psychology*, 72, 218–232.
- Elliot, A. J., & Thrash, T. M. (2002). Approach-avoidance motivation in personality: Approach-avoidance temperaments and goals. *Journal of Personality and Social Psychology*, 82, 804–818.
- Eysenck, H. J. (1967). *The biological basis of personality*. Springfield, IL: Thomas.
- Eysenck, H. J. (1997). Personality and experimental psychology: The unification of psychology and the possibility of a paradigm. *Journal of Personality and Social Psychology*, 73, 1224–1237.
- Eysenck, H. J., & Eysenck, S. B. G. (1992). *The Eysenck Personality Questionnaire-Revised*. Sevenoaks, UK: Hodder & Stoughton.
- Francis, D., Diorio, J., Liu, D., Meaney, M. J. (1999). Nongenomic transmission across generations of maternal behavior and stress responses in the rat. *Science*, 286, 1155–1158.
- Furnham, A., & Jackson, C. (2008). Reinforcement sensitivity in the work-place: BIS/BAS in business. In P. J. Corr (Ed.), *The reinforcement sensitivity theory of personality*. Cambridge, UK: Cambridge University Press.
- Gillespie, N. A., Cloninger, C. R., Heath, A. C., & Martin, N. G. (2003). The genetic and environmental relationship between Cloninger's dimensions of temperament and character. *Personality and Individual Differences*, 35, 1931–1946.
- Goldberg, L. R. (1990). An alternative "description of personality": The big-five factor structure. *Journal of Personality and Social Psychology*, 59, 1216–1229.
- Gray, J. A. (1973). Causal models of personality and how to test them. In J. R. Royce (Ed.), *Multivariate analysis and psychological theory* (pp. 409–463). London, UK: Academic Press.
- Gray, J. A. (1981). A critique of Eysenck's theory of personality. In H. J. Eysenck (Ed.), *A model for personality* (pp. 246–276). Berlin: Springer.
- Gray, J. A. (1982). *Neuropsychological theory of anxiety: An investigation of the septal-hippocampal system*. Cambridge, UK: Cambridge University Press.

- Gray, J. A. (1985). A whole and its parts: Behaviour, the brain, cognition and emotion. *Bulletin of the British Psychological Society*, 38, 99–112.
- Gray, J. A. (1987). *The psychology of fear and stress*. Cambridge, UK: Cambridge University Press.
- Gray, J. A., & McNaughton, N. (2000). *The neuropsychology of anxiety: An enquiry into the functions of thesepto-hippocampal system* (2nd ed.). Oxford, UK: Oxford University Press.
- Gusnard, D. A., Ollinger, J. M., Shulman, G. L., Cloninger, C. R., Price, J. L., Van Essen, D. C., et al. (2003). Persistence and brain circuitry. *Proceedings of the National Academy of Sciences USA*, 100, 3479–3484.
- Haas, B. W., Omura, K., Constable, R. T., & Canli, T. (2007). Emotional conflict and neuroticism: Personality-dependent activation in the amygdala and subgenual anterior cingulate. *Behavioural Neuroscience*, 121, 249–256.
- Haefely, W. E., Martin, J. R., Richards, J. G., & Schoch, P. (1993). The multiplicity of actions of benzodiazepine receptor ligands. *Canadian Journal of Psychiatry*, 38, S102–S108.
- Hampton, A. N., Adolphs, R., Tyszka, M. J., & O'Doherty, J. P. (2007). Contributions of the amygdala to reward expectancy and choice signals in human prefrontal cortex. *Neuron*, 55, 545–555.
- Harmon-Jones, E., Lueck, L., Fearn, M., & Harmon-Jones, C. (2006). The effect of personal relevance and approach-related action expectation on relative left frontal cortical activity. *Psychological Science*, 17, 434–440.
- Heath, A. C., Cloninger, C. R., & Martin, N. G. (1994). Testing a model for the genetic structure of personality: A comparison of the personality systems of Cloninger and Eysenck. *Journal of Personality and Social Psychology*, 66, 762–775.
- Hosie, A. M., Wilkins, M. E., da Silva, H. M., & Smart, T. G. (2006). Endogenous neurosteroids regulate GABAA receptors through two discrete transmembrane sites. *Nature*, 444, 486–489.
- Jackson, C. J. (2003). Gray's reinforcement sensitivity theory: A psychometric critique. *Personality and Individual Differences*, 34, 533–544.
- Kable, J. W., & Glimcher, P. W. (2007). The neural correlates of subjective value during intertemporal choice. *Nature Neuroscience*, 10, 1625–1633.
- Knutson, B., & Cooper, J. C. (2005). Functional magnetic resonance imaging of reward prediction. *Current Opinion in Neurology*, 18, 411–417.
- LeDoux, J. E. (1998). *The emotional brain: The mysterious underpinnings of emotional life*. London: Phoenix.
- Leue, A., Chavanon, M.-L., Wacker, J., & Stemmler, G. On the differentiation of N2-components in an appetitive choice task. *Psychophysiology*. (submitted for publication).
- Lieberman, N., Molden, D. C., Idson, L. C., & Higgins, E. T. (2001). Promotion and prevention focus on alternative hypotheses: Implications for attributional functions. *Journal of Personality and Social Psychology*, 80, 5–18.
- Matthews, G. (2004). Neuroticism from the top down: Psychophysiology and negative emotionality. In R. Stelmack (Ed.), *On the psychobiology of personality: Essays in honor of Marvin Zuckerman* (pp. 249–266). Amsterdam, NL: Elsevier Science.
- Matthews, G. (2008a). Personality and information processing: A cognitive-adaptive theory. In G. J. Boyle, G. Matthews, & D. H. Saklofske (Eds.), *Handbook of personality theory and assessment: Vol. 1: Personality theories and models* (pp. 56–79). Thousand Oaks, CA: Sage.
- Matthews, G. (2008b). Reinforcement sensitivity theory: A critique from cognitive science. In P. J. Corr (Ed.), *The reinforcement sensitivity theory of personality*. Cambridge, UK: Cambridge University Press.
- Matthews, G., & Gilliland, K. (1999). The personality theories of H. J. Eysenck and J. A. Gray: A comparative review. *Personality and Individual Differences*, 26, 583–626.
- Matthews, G., Schwan, V. L., Campbell, S. E., Saklofske, D. H., & Mohamed A. A. R. (2000). Personality, self-regulation and adaptation: A cognitive-social framework. In M. Boekarts, P. R. Pintrich, & M. Zeidner (Eds.), *Handbook of self-regulation* (pp. 171–207). New York, NY: Academic Press.
- McNaughton, N. (1989). *Biology and emotion*. Cambridge, UK: Cambridge University Press.

- McNaughton, N., Kocsis, B., & Hajós, M. (2007). Elicited hippocampal theta rhythm: A screen for anxiolytic and pro-cognitive drugs through changes in hippocampal function? *Behavioural Pharmacology*, *18*, 329–346.
- Meaney, M. J., Tannenbaum, B., Francis, D., Bhatnagar, S., Shanks, N., Viau, V., et al. (1994). Early environmental programming hypothalamic-pituitary-adrenal responses to stress. *Seminal Neuroscience*, *6*, 247–259.
- Montgomery, S. A. (2008). The under-recognized role of dopamine in the treatment of major depressive disorder. *International Clinical Psychopharmacology*, *23*, 63–69.
- Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*, 483–522.
- Ortony, A., Norman, D. A., & Revelle, W. (2005). Effective functioning: A three level model of affect, motivation, cognition, and behavior. In J. Fellous, & M. Arbib (Eds.), *Who needs emotions? The brain meets the machine* (pp. 173–202). New York, NY: Oxford University Press.
- Panksepp, J. (1998). *Affective Neuroscience: The foundations of human and animal emotions*. London, UK: Oxford University Press.
- Pesola, F., & Pickering, A. D. (2006). The interaction between personality and payoff structure in category learning. *Paper Presented at the 13th European Conference on Personality*, Athens, 2006.
- Pickering, A. D. (2008). Formal and computational models of Reinforcement Sensitivity Theory. In P. J. Corr (Ed.) *The reinforcement sensitivity theory of personality*. Cambridge, UK: Cambridge University Press.
- Pickering, A. D., Corr, P. J., Powell, J. H., Kumari, V., Thornton, J. C., & Gray, J. A. (1997). Individual differences in reactions to reinforcing stimuli are neither black nor white: To what extent are they Gray? In H. Nyborg (Ed.), *The scientific study of human nature: Tribute to Hans J. Eysenck at eighty* (pp. 36–67). London, UK: Elsevier Sciences.
- Pickering, A. D., & Gray, J. A. (1999). The neuroscience of personality. In L. A. Pervin, & O. P. John (Eds.), *Handbook of personality: Theory and research* (2nd ed., pp. 277–299). New York, NY: Guilford Press.
- Pickering, A. D., & Gray, J. A. (2001). Dopamine, appetitive reinforcement, and the neuropsychology of human learning: An individual differences approach. In A. Elias, & A. Angleitner (Eds.), *Advances in individual differences research* (pp. 113–149). Lengerich, Germany: PABST Science Publishers.
- Pickering, A. D., & Smillie, L. D. (2008). The behavioural activation system: Challenges and opportunities. In P. J. Corr (Ed.), *The reinforcement sensitivity theory of personality*. Cambridge, UK: Cambridge University Press.
- Pizzagalli, D. A., Sherwood, R. J., Henriques, J. B., & Davidson, R. J. (2005). Frontal brain asymmetry and reward responsiveness. A source-localization study. *Psychological Science*, *16*, 805–813.
- Reuter, M., Schmitz, A., Corr, P., & Hennig, J. (2006). Molecular genetics support Gray's personality theory: The interaction of COMT and DRD2 polymorphisms predicts the behavioural approach system. *The International Journal of Neuropsychopharmacology*, *1*, 1–12.
- Reuter, M., Stark, R., Hennig, J., Walter, B., Kirsch, P., Schienle, A., & Vaitl, D. (2004). Personality and emotion: Test of Gray's personality theory by means of an fMRI study. *Behavioural Neuroscience*, *118*, 462–469.
- Revelle, W. (1993). Individual differences in personality and motivation: 'Non-cognitive' determinants of cognitive performance. In A. Baddeley, & L. Weiskrantz (Eds.), *Attention: Selection, awareness, and control: A tribute to Donald Broadbent* (pp. 346–373). New York, NY: Clarendon Press/Oxford University Press.
- Revelle, W. (2008). The contribution of reinforcement sensitivity theory to personality theory. In P. Corr (Ed.), *Reinforcement sensitivity theory of personality*. Cambridge, UK: Cambridge University Press.
- Reynolds, B., Ortengren, A., Richards, J. B., & de Wit, H. (2006). Dimensions of impulsive behavior: Personality and behavioral measures. *Personality and Individual Differences*, *40*, 305–315.
- Reynolds, J. N. J., Hyland, B. I., & Wickens, J. R. (2001). A cellular mechanism of reward-related learning. *Nature*, *413*, 67–70.
- Rothbart, M. K., & Posner, M. (1985). Temperament and the development of self-regulation. In L. C. Hartlage, & C. F. Telzrow, C. F. (Eds.), *The neuropsychology of individual differences: A developmental perspective* (pp. 93–123). New York, NY: Plenum.

- Rothbart, M. K., Ahadi, S. A., & Evans, D. E. (2000). Temperament and personality: Origins and outcomes. *Journal of Personality and Social Psychology*, *78*, 122–135.
- Schneirla, T. C. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In M. Jones (Ed.), *Nebraska symposium on motivation*. Lincoln, NB: University of Nebraska Press.
- Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of Neurophysiology*, *80*, 1–27.
- Schultz, W. (2007). Behavioural dopamine signals. *Trends in Neurosciences*, *30*, 203–210.
- Sieghart, W. (2006). Structure, pharmacology, and function of GABAA receptor subtypes. *Advances in Pharmacology*, *54*, 231–263.
- Simons, J. S., & Gaher, R. M. (2005). The Distress Tolerance Scale: Development and validation of a self-report measure. *Motivation and Emotion*, *29*, 83–102.
- Smillie, L. D., Pickering, A. D., & Jackson, C. J. (2006). The new reinforcement sensitivity theory: Implications for psychometric measurement. *Personality and Social Psychology Review*, *10*, 320–335.
- Soubrié, P. (1986). Reconciling the role of central serotonin neurons in human and animal behavior. *Behavioral and Brain Sciences*, *9*, 319–364.
- Spoont, M. R. (1992). Modulatory role of serotonin in neural information processing: Implications for human psychopathology. *Psychological Bulletin*, *112*, 330–350.
- Stein, M. B., Schork, N. J., & Gerlenter, J. (2008). Gene-by-environment (serotonin transporter and childhood maltreatment) interaction for anxiety sensitivity, an intermediate phenotype for anxiety disorders. *Psychoneuropharmacology*, *33*, 312–319.
- Sullivan, R. N., Landers, M., Yeaman, B., & Wilson, D. (2000). Good memories of bad events in infancy. *Nature*, *407*, 38–39.
- Tanji, J., & Hoshi, E. (2008). Role of the lateral prefrontal cortex in executive behavioral control. *Physiological Reviews*, *88*, 37–57.
- Taylor, S., Zvolensky, M. J., & Cox, B. J. (2007). Robust dimensions of anxiety sensitivity: Development and initial validation of the Anxiety Sensitivity Index-3. *Psychological Assessment*, *19*, 176–188.
- Tellegen, A., Watson, D., & Clark, L. A. (1999). On the dimensional and hierarchical structure of affect. *Psychological Science*, *10*, 297–303.
- Torrubia, R., Avila, C., Molto, J., & Caseras, X. (2001). The sensitivity to punishment and sensitivity to reward questionnaire as a measure of Gray's anxiety and impulsivity dimensions. *Personality and Individual Differences*, *31*, 837–862.
- Torrubia, R., Ávila, C., & Caseras, X. (2008). Reinforcement sensitivity scales. In P. J. Corr (Ed.), *The reinforcement sensitivity theory of personality*. Cambridge, UK: Cambridge University Press.
- Triesman, U. (1992). Studying students studying calculus: A look at the lives of minority mathematics students in college. *The College Mathematics Journal*, *23*, 362–372.
- Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, *53*, 1–25.
- Turkheimer, E. (2000). Three laws of behavior genetics and what they mean. *Current Directions in Psychological Science*, *9*, 160–164.
- Turner, R. M., Hudson, I. L., Butler, P. H., & Joyce, P. R. (2003). Brain function and personality in normal males: A SPECT study using statistical parametric mapping. *NeuroImage*, *19*, 1145–1162.
- van Overveld, W. J. M., de Jong, P. J., Peters, M. L., Cavanaugh, K., & Davies, G. C. L. (2006). Disgust prosensivity and disgust sensitivity: Separate constructs that are differentially related to specific fears. *Personality and Individual Differences*, *41*, 1241–1253.
- Wacker, J., Chavanon, M.-L., Leue, A., & Stemmler, G. (2008). Is running away right? The behavioral activation—behavioral inhibition model of anterior asymmetry. *Emotion*, *8*, 232–249.
- Wacker, J., Heldmann, M., & Stemmler, G. (2003). Separating emotion and motivational direction in fear and anger: Effects on frontal asymmetry. *Emotion*, *3*, 167–193.
- Watson, D., & Clark, L. A. (1992). On traits and temperament: General and specific factors of emotional experience and their relation to the five-factor model. *Journal of Personality*, *60*, 441–476.

- Weaver, I. C. G., Cervoni, N., Champagne, F. A., D'Alessio, A. C., Sharma, S., Seckl, J. R., et al. (2004). Epigenetic programming by maternal behavior. *Nature Neuroscience*, *7*, 847–854.
- Weiner, B., & Schneider, K. (1971). Drive vs. cognitive theory: A reply to Boor and Harmon. *Journal of Personality and Social Psychology*, *8*, 258–262.
- 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.
- Winston J. S., O'Doherty J., Kilner J. M., Perrett D. I., Dolan R. J. (2007). Brain systems for assessing facial attractiveness. *Neuropsychologia*, *45*, 195–206.
- Zuckerman, M. (1991). *Psychobiology of personality*. New York, NY: Cambridge University Press.
- Zuckerman, M., & Cloninger, C. R. (1996). Relationships between Cloninger's, Zuckerman's, and Eysenck's dimensions of personality. *Personality and Individual Differences*, *21*, 283–285.