

Contents lists available at ScienceDirect

Personality and Individual Differences

journal homepage: www.elsevier.com/locate/paid



The evolution of the Behavioural Approach System (BAS): Cooperative and competitive resource acquisition strategies



Dino Krupić^{a,*}, Asmir Gračanin^b, Philip J. Corr^c

^a Department of Psychology, University of J.J. Strossmayer in Osijek, Osijek, Croatia

^b Department of Psychology, University of Rijeka, Rijeka, Croatia

^c Department of Psychology, City University London, London, UK

ARTICLE INFO

Article history: Received 11 November 2015 Received in revised form 23 January 2016 Accepted 25 January 2016 Available online xxxx

Keywords: Reinforcement sensitivity theory Motivation Personality Evolution Set correlation analysis

ABSTRACT

The nature of approach motivation has not yet been adequately defined. Some authors view it as a unidimensional construct, while others consider it to be multidimensional. Its psychometric nature is explored in this study, which tests empirically the motivational account of the Behavioural Approach System (BAS) within an evolutionary context. In a sample of 394 participants, we administered the Assessment of Individual Motives questionnaire (AIM-Q), the Reinforcement Sensitivity Theory Personality Questionnaire (RST-PQ) and a short version of the Sensitivity to Punishment and Sensitivity to Reward (SPSRQ-20). The results of set correlation analysis indicated that different BAS scales relate to different motives, thus supporting the multidimensional perspective on approach motivation. Specifically, Reward Interest relates to various types of motives that generally reflect sensitivity to social rewards; Goal-Drive Persistence relates to social exchange; Reward Reactivity to safety and commitment; while Impulsivity and Sensitivity to Reward (SR) relate to competitive motives. These results are discussed within an evolutionary framework for the multidimensionality of the BAS.

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1. Introduction

The Behavioural Approach System (BAS) is one of the three major systems in the neuropsychological theory of personality known as the reinforcement sensitivity theory (RST), which includes two additional defensive systems: the Fight-Flight-Freeze System (FFFS), responsible for the active avoidance of, and escape from, aversive stimuli; and the Behavioural Inhibition System (BIS), responsible for passive avoidance and the detection and resolution of goal-conflict. It is assumed that the BAS represents a general domain approach mechanism designed to solve the important evolutionary adaptive problem of attaining critical resources, such as food, water, sex and social status (Berridge, 2004; Berridge & Robinson, 2003; Kenrick & Shiota, 2008). In general terms, the BAS mediates reactions to reward and non-punishment. Its outputs serve to motivate approach behaviours toward biological reinforcers and to engage in activities that lead to consummatory behaviour (Corr, 2008; Gray & McNaughton, 2000). Despite the popularity and long history of this theory, the obvious evolutionary importance of the BAS has not yet been explored empirically.

E-mail address: dkrupic@ffos.hr (D. Krupić).

2. Evolutionary explanations of individual differences

Within evolutionary psychology, individual differences in personality and/or temperament are interpreted as variations in adaptive mechanisms that evolved to provide solutions to problems concerning reproduction and survival (Buss, 2008, 2009). Since environmental conditions were not equal for the entire human population, it may be assumed that some phenotypic variations were more adaptive in one environment than in another. Thus, there is no "gold standard" for a personality trait that could provide the best possible fitness in every environment (Penke, 2010; Penke, Denissen, & Miller, 2007). Therefore, it is reasonable to assume the existence of a variety of resource acquisition strategies which could ensure flexible and adaptive behaviour in different environmental conditions.

We can distinguish two main groups of resource acquisition strategies developed in social species: competition (e.g., stealing, trickery, aggression) and cooperation (e.g., social exchange, altruism) (Buss, 1999). Competitive strategies are mostly related to questions of social hierarchy, status, or power, with individuals ranking higher on the social scale having access to more resources whilst facing lower risks and required effort. In contrast, cooperative strategies are seen as mutually beneficial (Scott-Phillips, Dickins, & West, 2011). On a proximal level, cooperation can be manifested as volunteering, social exchange, reciprocal altruism, and so on (Buss, 1999; Tooby & Cosmides, 1988). We can assume that cooperative behaviour is driven by the need for

^{*} Corresponding author at: Department of Psychology, Faculty of Humanities and Social Sciences, University of J. J. Strossmayer in Osijek, Osijek, Croatia.

social approval, which is a very powerful incentive (e.g., Izuma, Saito, & Sadato, 2010), and it serves the function of attaining social status. In economics, this is known as the 'public good' benefit. As such, helping others may be seen as an investment or even buying insurance for future events in which one would seek help from the same individuals. Which of these two strategies would be used, depends upon environmental conditions and individual differences.

The aim of this study is to examine empirically, for the first time, which of these two evolved resource acquisition strategies are related to individual differences in the BAS. We expect the BAS to correlate with variation in both cooperative and competitive strategies, as reflected in different motives that are expected to fuel the exertion of these strategies.

The heterogeneity of the BAS may derive from the 'arms race' between predator and prey. The 'Life-Dinner Principle' (Dawkins & Krebs, 1979) suggests that the evolutionary selective pressure on the prey is much stronger than on the predator: if a predator fails to kill its prey, it has lost its dinner, but if the prey fails to avoid/escape being the predator's dinner, then it has lost its life. Although defensive behaviours, principally freezing, fleeing and defensive attack, are themselves relatively complex (Eilam, 2005), it is nonetheless true that the behaviour of the prey is intrinsically simpler than that of the predator: all it has to do is avoid/escape, making it, guite literally, life-or-death behaviour (Corr, 2008). In contrast, the predator has to develop counterstrategies to meet its BAS aims, which entail a higher degree of cognitive and behavioural sophistication over the prey's defensive behavioural repertoire. Another reason for the complexity of the BAS comes from heterogeneity of appetitive goals (e.g., securing food and finding/keeping a sexual mate), which demand a corresponding heterogeneity of BAS-related strategies.

The putative multidimensional nature of the BAS is also grounded in the neurobiology of personality, which recognizes two approach related traits: impulsivity and extraversion, that are related to different neurotransmitters. Impulsivity is associated with dopamine, serotonin (Dalley & Roiser, 2012), and testosterone (Montoya, Terburg, Bos, & van Honk, 2012). Testosterone has been found important in attaining social status in number of cross-species studies (e.g., Beaver & Amoss, 1982; Coe, Mendoza, & Levine, 1979; Elofsson, Mayer, Damsgård, & Winberg, 2000). In human studies, testosterone is linked with domination (Sellers, Mehl, & Josephs, 2007), choice of risky carriers (Sapienza, Zingales, & Maestripieri, 2009), aggression (Archer, 2006), and level of reproductive effort (Alvergne, Jokela, Faurie, & Lummaa, 2010), which all correspond to competitive motives. Thus, we may expect that the RST scales reflecting impulsivity (the SR and RST-Impulsivity) should correlate with competitive motives.

Neurobiologically, nurturance/cooperativeness is based on oxytocin system functions (e.g., Feldman, 2012; Yamasue et al., 2008). The second candidate for the neurobiological underpinnings of nurturance/cooperation are endogenous opiates, which are involved in the positive emotions that follow attainment or consumption of reward. This is a key feature of Reward Reactivity, and is important in social affiliation, making opiates likely candidates for a biological substrate of Extraversion and Social Closeness (Berridge, 2012; Depue & Morrone-Strupinsky, 2005). Thus, we may expect that the RST-PQ scales designed closely to extraversion (Reward Interest, Goal-Drive Persistence, and Reward Reactivity) should correlate more with the cooperative motives.

3. Materials and methods

3.1. Participants and procedure

A total of 394 (208 male and 186 female) participants ($M_{AGE} = 27.99$; SD = 9.70, range from 16 to 54) completed three questionnaires online using LimeSurvey web application. Only complete data were recorded. The Ethics Committee of Faculty of Humanities and Social Sciences in Rijeka gave approval for the study

3.2. Measures

We administered two RST questionnaires: Reinforcement Sensitivity Theory Personality Questionnaire (RST-PQ; Corr & Cooper, 2016), and the Sensitivity to Punishment and Sensitivity to Reward Questionnaire-20 (SPSRQ-20; Aluja & Blanch, 2011; Torrubia, Avila, Molto, & Caseras, 2001). We also administered the Assessment of Individual Motives (AIM-Q; Bernard, 2013) which provides a measure for cooperative and competitive resource acquisition strategies and integrity motives.

The RST-PQ (Corr & Cooper, 2016) contains 65 items for measuring the BAS, the Behavioural Inhibition System (BIS) and Fight/Flight/Freeze System (FFFS). The BAS consists of four sub-scales. People that score high on Reward Interest scale (seven items) are more likely to engage in anticipatory approach, exploration of new objects, places and people (e.g., "I regularly try new activities just to see if I enjoy them"). Goal-Drive-Persistence (seven items) measures the persistence in achieving the ultimate aim of obtaining a reward (e.g., "I put in a big effort to accomplish important goals in my life"). Reward Reactivity (ten items) relates to the level of experiencing emotional reaction to reward (i.e., 'pleasure') and provides the positive reinforcement for BAS behaviour (e.g., "Good news makes me feel over-joyed"). Finally, Impulsivity (eight items) refers to the final stage of catching the biological reinforcer, where nonplanning and fast reactions are more appropriate (e.g., "I think I should 'stop and think' more instead of jumping into things too quickly"). Using the criterion of Hu and Bentler (1999), the four-factor model of the BAS in this study showed adequate goodness of fit indices ($\chi^2/df =$ 2.71, CFI = .903; RMSEA = .066). Internal reliability coefficients (Cronbach's alpha) are 0.75 for Reward Interest, 0.83 for Goal-Drive Persistence, 0.75 for Reward Reactivity, and 0.67 for Impulsivity.

The SPSRQ-20 (Aluja & Blanch, 2011; Torrubia et al., 2001) measures Sensitivity to Reward (SR; e.g., "Do you like being the centre of attention at a party or a social meeting") and Sensitivity to Punishment (SP; e.g., "Are you often afraid of new or unexpected situations?"); each scale containing 10 items. Reliability coefficients are 0.66 for SR and 0.82 for SP.

The Croatian translation of both questionnaires was validated earlier (Krupić, Križanić, Ručević, Gračanin, & Corr, 2016). Data for the defensive BIS, FFFS, Defensive fight (for the RST-PQ) and the SP (for the SPSRQ) were also collected, but as they are out of scope of this study they were not analysed.

AIM-Q (Bernard, 2013) is a 60-item questionnaire that measures 15 human-specific motives (Bernard, 2009, 2010) within the evolutionary theory of human motivation (Bernard, Mills, Swenson, & Walsh, 2005). Each motive is represented by four items answered on a seven point Likert-type scale. Bernard (2013) distinguishes three types of motives: (a) motives facilitating individual integrity (Environmental Inquisitiveness, Threat Avoidance, Illness Avoidance); (b) motives facilitating competition for resources and mates (Interpersonal Inquisitiveness, Aggression, Appearance, Mental, Physical, Wealth, Sex); and (c) motives facilitating cooperation in order to gain resources (Commitment, Kin Altruism, Social exchange, Legacy and Meaning). Full description of the questionnaire and constructs can be found in Bernard and Lac (2014). Reliability coefficients are presented in Table 1. Generally, all except Illness avoidance achieve reliability above .70.

3.3. Analytic plan

Relationships between the BAS scales and AIM-Q motives were analysed by set correlation analysis (SCA), which provides the statistical control for a set of research factors (in our case gender and age), when relating one set of variables (in our case the BAS scales) to another (in our case 15 AIM-Q motives). In this way, confounding variables are held under control, and the likelihood of Type I error is reduced, which promotes the uniqueness of relationship between variables (Cohen, Cohen, Aiken, & West, 2003). Statistical control of gender and age is important in determining the unique adaptive account of the BAS, since they represent an important source of variation within the Descriptive statistics and results of set correlation analysis between AIM-Q motives and approach dimensions of SPSRQ-20 and RST-PQ controlled for gender and age.

	Motives facilitating individual integrity			Motives facilitating cooperation					Motives facilitating competition for resources and mates						
	THA	ILA	EIQ	COM	KIN	SOC	LEG	MEA	AGG	INI	SEX	APP	WEA	MEN	PHY
Gender	.01	03	.24**	.09	07	.05	.12	.11	01	08	27**	.18**	11	.02	17**
Age	.06	.05	.01	04	09	.06	.05	.05	07	11	.06	.04	00	07	.02
Reward interest	08	11	.44**	02	.22**	.15	.32**	.32**	01	07	.00	.04	10	01	.25**
Goal-drive persistence	e .07	.02	.07	.02	04	.23**	03	08	05	08	14	03	.01	.10	.06
Reward reactivity	.26**	.14	00	.18**	.02	.14	.04	06	11	.03	02	04	.05	.01	04
Impulsivity	04	.02	.07	.08	.12	07	.06	.03	.21**	.22**	.17**	.06	.12	.01	11
Sensitivity to reward	l –.19 ^{**}	.17**	11	13	10	23**	09	00	.32**	.24**	.19**	.37**	.41**	.49**	.36**
M	15.49	12.29	17.96	18.11	16.03	20.25	12.36	11.98	6.84	10.53	8.60	6.64	6.75	10.63	10.97
SD	4.217	3.738	4.025	4.987	4.033	2.621	4.966	5.822	3.357	5.161	4.218	3.446	3.554	4.552	5.257
α	.73	.58	.87	.91	.75	.72	.87	.93	.80	.91	.85	.80	.84	.83	.89
R	.29	.23	.56	.26	.28	.44	.38	.29	.43	.42	.43	.38	.49	.53	.51
R ²	.086	.053	.318	.067	.079	.197	.143	.084	.183	.176	.186	.148	.239	.283	.262
F (7, 386)	5.20**	3.09**	25.71**	3.98**	4.74**	13.51**	9.19**	5.05**	12.37**	11.74**	12.60**	9.57**	17.29**	21.75**	19.58**

 α – Cronbach alpha; R – multiple correlation coefficient; R² – multiple determination coefficient; THA – Threat Avoidance; ILA – Illness Avoidance; EIQ – Environmental Inquisitiveness; COM – Commitment; KIN – Kin Altruism; SOC – Social; Exchange; LEG – Legacy; MEA – Meaning; positive correlation for Gender indicates higher score for males. AGG – Aggression; INI – Interpersonal Inquisitiveness; SEX – Sex; APP – Appearance; WEA – Wealth; MN – Mental; PH – Physical; positive correlation for Gender indicates higher score for males. ** p < 0.01.

evolutionary psychology. Additionally, we used Bonferroni correction in determining the statistical significance in order to reduce further Type I error due to a larger number of correlations tested.

4. Results

Descriptive statistics for AIM-Q and results of SCA are shown in Table 1, while zero order correlation matrices between and within questionnaires are available in *Supplementary materials*. All analyses were conducted using R version 3.2.2 (R Development Core Team, 2013), using package psych version 1.5.8 (Revelle, 2015).

Using set correlation, all canonical variates in the data set were taken into account in one index to provide an overall estimate of association. The overall relationship between personality traits and motives using Cohen's Set Correlation was $R^2 = .82$, which was statistically significant F(6.75, 105) = 2294.39, p < 0.01. Weak to moderate relationships $(R^2 = .05-.32)$ were found between discrete motives and personality traits. Further, different patterns of partial correlations for AIM-Q motives, controlled for gender and age, were shown among BAS scales. In general, the SR and Impulsivity were more related with competitive, while Reward Interest, Goal-Drive Persistence and Reward Reactivity were more related with cooperative motives, as expected. Reward interest was related with Kin Altruism, Meaning, Legacy, but also with Physical and Environmental Inquisitiveness, that belongs to competitive and integrity motives, respectively. Goal-Drive Persistence was related with Social exchange, while Reward Reactivity showed links with Commitment from cooperative group of motives, and Threat avoidance from Integrity motives.

5. Discussion

In order to provide an evolutionary account of the BAS, we examined the relationships between inter-individual variation on different BAS scales and different types of motives, including (a) motives facilitating individual integrity, (b) motives facilitating competition for resources and mates, and (c) motives facilitating cooperation. Overall, the BAS scales correlated with both resource acquisition strategies and, additionally, with the integrity motives. More specifically, discrete motives are found to correlate with different aspects of the BAS functioning. This suggests that different aspects of the BAS were shaped throughout evolutionary history in order to confront specific adaptive problems. Put simply, while the AIM-Q detects *what* were the adaptive goals, the BAS explains *how* these goals were obtained. Weak to moderate relationships were found between discrete motives and personality traits, which is reasonable since motives and personality traits are not equivalent constructs. Motives are defined as a predisposition to behave in a directed fashion, focusing on behaviour solely, while personality traits are defined as complex constructs combining stable behavioural, cognitive and emotional characteristics (for details see Bernard & Lac, 2014). Thus, low to moderate correlations between the BAS scales and motives are expected.

Reward Interest correlated with the tendency of exploring the environment (Environmental inquisitiveness), participating in competitions that signal gender-appropriate physical ascendancy (Physical), caring for relatives (Kin Altruism), and with reciprocation among non-kin (Legacy and Meaning). In general, individuals that score high on Reward Interest scale show a tendency to act prosocially, or to contribute to society.

The next finding relates Goal-Drive Persistence with tendency to enter into reciprocal, mutually beneficial exchanges of resources with non-kin (Social Exchange). The cooperation is more of a long-term strategy (Barclay, 2013; Stevens, Cushman, & Hauser, 2005). It takes time to build trust between people, and even then, it is not certain whether it will be mutually beneficial. Therefore, it is not surprising that many studies show that reward delay capacity is important in maintaining cooperative behaviour (Brosnan, Salwiczek, & Bshary, 2010; Kortenkamp & Moore, 2006; Rosati, Stevens, Hare, & Hauser, 2007), which is the core feature of Goal-Drive Persistence.

Individuals high on Reward Reactivity scales show tendency toward maintaining one's safety (Threat Avoidance) and a greater capacity for developing tender, intimate, supportive attachments with mates and off-spring (Commitment). Reward Reactivity relates to emotional reactions to the final attainment of a desired goal. It serves as "emotional fuel" for the previous BAS processes (Corr & Cooper, 2016). Positive outcome followed by positive emotional reaction serves as reinforcement of invested effort in attaining a desired goal. According to our results, these processes have the importance in maintaining safety and a relationship with others.

Compared to cooperation, competition as a resource acquisition strategy is a more short-term strategy (Barclay, 2013; Stevens et al., 2005). RST-PQ Impulsivity relates with motives such as achieving domination (Aggression), tendency of mocking others, being sarcastic (Interpersonal Inquisitiveness), and searching for mates (Sex). In addition, individuals high on SR are more willing to display intellectual and physical superiority (Mental and Physical, respectively), material resources (Wealth), and to invest resources in order to look well (Appearance). In general, a common feature of individuals that score high on RST-PQ Impulsivity and the SR is a tendency to represent themselves as better than others. However, it is important to emphasize the difference between SR and Impulsivity (RST-PO), which appeared in our results. While Impulsivity relates exclusively to competitive motives, SR additionally correlates with integrity motives (Illness avoidance and Threat avoidance) and negatively with Social Exchange. Furthermore, the Impulsivity scale contains items that reflect tendencies of acting fast without thinking and not planning, thus reflecting poor executive function (e.g., "I think I should 'stop and think' more instead of jumping into things too quickly"). On the other hand, the SR contains items relating to behavioural tendencies (e.g., "When you are in a group, do you try to make your opinions the most intelligent or the funniest?"). The AIM-Q items are also designed to measure motivational tendencies on a behavioural level (e.g., "I show off my understanding of abstract or complex ideas so people will respect me"), which could result in common method variance with the SR, and thus spuriously increases correlation coefficients. Hence, we cannot discuss the relative importance of these two scales in competitiveness within this study, since they obviously measure different aspects of impulsivity.

The rest of associations were not significant, although zero-order correlation matrix in *Supplementary materials* might suggest the opposite. This discrepancy suggests that the BAS scales correlate with some other motives as well, but these relations are confounded, since both — the BAS scales and the motives — are highly inter-correlated. Thus, the discrepancy of the results represents the ability of SCA to detect confounding effects between two sets of variables. This way, the SCA provides a unique relationship between two variables, when many other variables are held under statistical control, and these effects are very likely to replicate.

Most of the empirical work in the original version of the RST was based on animal studies, particularly rodents. Upon these experiments, the idea of the unidimensional BAS could seem very plausible. However, as we can see, different adaptive goals demand different strategies of the BAS. We believe that the BAS complexity arises from highly complex human environment in comparison to rodents'— which has not been taken into account in the original version of RST.

The findings of this study hold significance in understanding the differences that are commonly observed between the various BAS scales (e.g. Jackson & Smillie, 2004; Krupić & Corr, 2014; Smillie, Jackson, & Dalgleish, 2006). Understanding the conceptual differences between the BAS scales could lead toward setting more precise hypotheses in RST studies. However, much work is needed in order to produce a complete picture of the evolutionary origins of the BAS. Further studies should focus on sex dimorphism and relationships between different aspects of the BAS functioning and variables such as relationship instability, sociosexuality, and parental effort, which are important for understanding its adaptive functions.

The major limitation of this study concerns the usage of only one psychometric measure for competitive and cooperative motives, and the study design that does not allow for causal interpretation. Furthermore, we did not include the BIS and FFFS scales in our study, what might have influenced the results. Currently, the theory is not clear whether the approach and avoidance system function separately, or they have mutually inhibitory effects, which is beyond the scope of this paper (*however*, *reanalysed data can be found in Supplementary materials*).

In conclusion, the results of this study show that impulsivity, as measured by RST-PQ and SR from SPSRQ, relates to competitive, Goal-Drive Persistence and Reward Reactivity relate to cooperative, while Reward Interest relates to both resource acquisition strategies, which altogether represent a set of novel findings in RST research. Clearly, the evolutionary perspective provides a coherent theoretical account of the multidimensionality of approach motivation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.paid.2016.01.044.

References

- Aluja, A., & Blanch, A. (2011). Neuropsychological Behavioral Inhibition System (BIS) and behavioral approach system (BAS) assessment: A shortened Sensitivity to Punishment and Sensitivity to Reward Questionnaire version (SPSRQ–20). Journal of Personality Assessment, 93(6), 628–636. http://dx.doi.org/10.1080/00223891.2011. 608760.
- Alvergne, A., Jokela, M., Faurie, C., & Lummaa, V. (2010). Personality and testosterone in men from a high-fertility population. *Personality and Individual Differences*, 49, 840–844. http://dx.doi.org/10.1016/j.paid.2010.07.006.
- Archer, J. (2006). Testosterone and human aggression: An evaluation of the challenge hypothesis. *Neuroscience and Biobehavioral Reviews*, 30, 319–345. http://dx.doi.org/10. 1016/j.neubiorev.2004.12.007.
- Barclay, P. (2013). Strategies for cooperation in biological markets, especially for humans. Evolution and Human Behavior, 34, 164–175. http://dx.doi.org/10.1016/j. evolhumbehav.2013.02.002.
- Beaver, B., & Amoss jr, M. (1982). Aggressive behavior associated with naturally elevated serum testosterone in mares. *Applied Animal Ethology*, 8, 425–428. http://dx.doi.org/ 10.1016/0304-3762(82)90055-4.
- Bernard, L. C. (2009). Consensual and behavioral validity of a measure of adaptive individual differences dimensions in human motivation. *Motivation and Emotion*, 33, 303–319. http://dx.doi.org/10.1007/s11031-009-9131-7.
- Bernard, L. C. (2010). Motivation and personality: Relationships between putative motive dimensions and the five factor model of personality. *Psychological Reports*, 106, 613–631. http://dx.doi.org/10.2466/PR0.106.2.613-631.
- Bernard, L. C. (2013). Manual for the Assessment of Individual Motives–Questionnaire. Unpublished manuscript, Loyola Marymount University, Los Angeles, CA.
- Bernard, L. C., & Lac, A. (2014). The incremental validity of motive traits of action: Predicting behavior longitudinally. *Individual Differences Research*, 12, 79–100.
- Bernard, L. C., Mills, M., Swenson, L., & Walsh, R. P. (2005). An evolutionary theory of human motivation. *Genetic, Social, and General Psychology Monographs*, 131, 129–184. http://dx.doi.org/10.3200/MON0.131.2.129-184.
- Berridge, K. C. (2004). Motivation concepts in behavioral neuroscience. *Physiology and Behavior*, 81, 179–209. http://dx.doi.org/10.1016/j.physbeh.2004.02.004.
- Berridge, K. C. (2012). From prediction error to incentive salience: Mesolimbic computation of reward motivation. *European Journal of Neuroscience*, 35, 1124–1143. http:// dx.doi.org/10.1111/j.1460-9568.2012.07990.x.
- Berridge, K. C., & Robinson, T. E. (2003). Parsing reward. Trends in Neurosciences, 26, 507–513. http://dx.doi.org/10.1016/S0166-2236(03)00233-9.
- Brosnan, S. F., Salwiczek, L, & Bshary, R. (2010). The interplay of cognition and cooperation. Philosophical Transactions of the Royal Society, B: Biological Sciences, 365(1553), 2699–2710. http://dx.doi.org/10.1098/rstb.2010.0154.
- Buss, D. M. (1999). Evolutionary psychology. London: Allyn and Bacon.
- Buss, D. M. (2008). Human nature and individual differences: Evolution of human personality. In O. P. John, R. W. Robins, & L. A. Pervin (Eds.), *Handbook of personality theory* and research (pp. 29–60) (3rd ed.). New York: Guilford Press.
- Buss, D. M. (2009). How can evolutionary psychology successfully explain personality and individual differences? *Perspectives on Psychological Science*, 4, 359–366. http://dx.doi. org/10.1111/j.1745-6924.2009.01138.x.
- Coe, C. L., Mendoza, S. P., & Levine, S. (1979). Social status constrains the stress response in the squirrel monkey. *Physiology and Behavior*, 23, 633–638. http://dx.doi.org/10.1016/ 0031-9384(79)90151-3.
- Cohen, J., Cohen, P., Aiken, L. S., & West, S. G. (2003). Applied multiple regression/correlation analysis for the behavioural sciences (3rd ed.). London: Erlbaum.
- Corr, P. J. (2008). Reinforcement sensitivity theory (RST): Introduction. In P. J. Corr (Ed.), The reinforcement sensitivity theory and personality (pp. 155–187). Cambridge: Cambridge University Press.
- Corr, P. J., & Cooper, A. (2016). The Corr-Cooper Reinforcement Sensitivity Theory Personality Questionnaire (RST-PQ): Development and validation. *Psychological Assessment*. http://dx.doi.org/10.1037/pas0000273 (in press).
- Dalley, J. W., & Roiser, J. P. (2012). Dopamine, serotonin and impulsivity. Neuroscience, 215, 42–58. http://dx.doi.org/10.1016/j.neuroscience.2012.03.065.
- Dawkins, R., & Krebs, J. R. (1979). Arms races between and within species. Proceedings of the Royal Society of London. Series B, Containing Papers of a Biological Character. Royal Society (Great Britain), 205(1161), 489–511. http://dx.doi.org/10.1098/rspb.1979.0081.
- Depue, R. A., & Morrone-Strupinsky, J. V. (2005). A neurobehavioral model of affiliative bonding: implications for conceptualizing a human trait of affiliation. *The Behavioral* and Brain Sciences, 28, 313–350. http://dx.doi.org/10.1017/S0140525X05000063 (discussion 350–395).
- Eilam, D. (2005). Die hard: A blend of freezing and fleeing as a dynamic defense Implications for the control of defensive behavior. *Neuroscience and Biobehavioral Reviews*, 29, 1181–1191. http://dx.doi.org/10.1016/j.neubiorev.2005.03.027.
- Elofsson, U. O., Mayer, İ., Damsgård, B., & Winberg, S. (2000). Intermale competition in sexually mature arctic charr: Effects on brain monoamines, endocrine stress responses, sex hormone levels, and behavior. *General and Comparative Endocrinology*, 118, 450–460. http://dx.doi.org/10.1006/gcen.2000.7487.
- Feldman, R. (2012). Oxytocin and social affiliation in humans. Hormones and Behavior, 61, 380–391. http://dx.doi.org/10.1016/j.yhbeh.2012.01.008.
- Gray, J. A., & McNaughton, N. (2000). The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system. New York: Oxford University Press.
- Hu, L. T., & Bentler, P. M. (1999). Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. *Structural Equation Modeling: A Multidisciplinary Journal*, 6, 1–55. http://dx.doi.org/10.1080/10705519909540118.
- Izuma, K., Saito, D. N., & Sadato, N. (2010). Processing of the incentive for social approval in the ventral striatum during charitable donation. *Journal of Cognitive Neuroscience*, 22, 621–631. http://dx.doi.org/10.1162/jocn.2009.21228.

- Jackson, C. J., & Smillie, L. D. (2004). Appetitive motivation predicts the majority of personality and an ability measure: A comparison of BAS measures and a re-evaluation of the importance of RST. *Personality and Individual Differences*, 36, 1627–1636. http://dx.doi.org/10.1016/j.paid.2003.06.010.
- Kenrick, D. T., & Shiota, M. N. (2008). Approach and avoidance. In A. J. Elliot (Ed.), Handbook of approach and avoidance motivation (pp. 273–288). New York: Psychology Press.
- Kortenkamp, K. V., & Moore, C. F. (2006). Time, uncertainty, and individual differences in decisions to cooperate in resource dilemmas. *Personality and Social Psychology Bulletin*, 32, 603–615. http://dx.doi.org/10.1177/0146167205284006.
- Krupić, D., & Corr, P. J. (2014). Individual differences in emotion elicitation in university examinations: A quasi-experimental study. *Personality and Individual Differences*, 71, 176–180. http://dx.doi.org/10.1016/j.paid.2014.08.001.
- Krupić, D., Križanić, V., Ručević, S., Gračanin, A., & Corr, P. J. (2016). Five reinforcement sensitivity theory (RST) of personality questionnaires: Comparison, validity and generalization. (in submission).
- Montoya, E. R., Terburg, D., Bos, P. A., & van Honk, J. (2012). Testosterone, cortisol, and serotonin as key regulators of social aggression: A review and theoretical perspective. *Motivation and Emotion*, 36, 65–73. http://dx.doi.org/10.1007/s11031-011-9264-3.
- Penke, L. (2010). Bridging the gap between modern evolutionary psychology and the study of individual differences. In D. M. Buss, & P. H. Hawley (Eds.), *The evolution of personality and individual differences* (pp. 243–279). New York: Oxford University Press. http://dx.doi.org/10.1093/acprof:oso/9780195372090.003.0009.
- Penke, L, Denissen, J. J. A., & Miller, G. F. (2007). The evolutionary genetics of personality. European Journal of Personality, 21, 549–587. http://dx.doi.org/10.1002/per.629.
- R Development Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Vienna, Austria: R Foundation for Statistical Computing (URL http://www.R-project.org/).
- Revelle, W. (2015). Psych: Procedures for Personality and Psychological Research. Evanston, Illinois, USA: Northwestern University (http://CRAN.R-project.org/package=psych). Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2007). The evolutionary origins of
- Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2007). The evolutionary origins of human patience: Temporal preferences in chimpanzees, bonobos, and human adults. *Current Biology*, 17, 1663–1668. http://dx.doi.org/10.1016/j.cub.2007.08.033.

- Sapienza, P., Zingales, L., & Maestripieri, D. (2009). Gender differences in financial risk aversion and career choices are affected by testosterone. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 15268–15273. http://dx.doi. org/10.1073/pnas.0907352106.
- Scott-Phillips, T. C., Dickins, T. E., & West, S. A. (2011). Evolutionary theory and the ultimate-proximate distinction in the human behavioral sciences. *Perspectives on Psychological Science*, 6, 38–47. http://dx.doi.org/10.1177/1745691610393528.
- Sellers, J. G., Mehl, M. R., & Josephs, R. A. (2007). Hormones and personality: Testosterone as a marker of individual differences. *Journal of Research in Personality*, 41, 126–138. http://dx.doi.org/10.1016/j.jrp.2006.02.004.
- Smillie, L. D., Jackson, C. J., & Dalgleish, L. I. (2006). Conceptual distinctions among Carver and White's (1994) BAS scales: A reward-reactivity versus trait impulsivity perspective. Personality and Individual Differences, 40, 1039–1050. http://dx.doi.org/10.1016/j. paid.2005.10.012.
- Stevens, J. R., Cushman, F. A., & Hauser, M. D. (2005). Evolving the psychological mechanisms for cooperation. Annual Review of Ecology, Evolution, and Systematics, 36, 499–518. http://dx.doi.org/10.1146/annurev.ecolsys.36.113004.083814.
- Tooby, J., & Cosmides, L. (1988). The evolution of war and its cognitive foundations. Institute for evolutionary studies technical report, 88(1). (pp. 1–15). Santa Barbara: Institute for Evolutionary Studies, University of California at Santa Barbara (Retrieved from http://www.cep.ucsb.edu/papers/EvolutionofWar.pdf).
- Torrubia, R., Avila, C., Molto, J., & Caseras, X. (2001). The Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ) as a measure of Gray's anxiety and impulsivity dimensions. *Personality and Individual Differences*, 31, 837–862. http://dx. doi.org/10.1016/S0191-8869(00)00183-5.
- Yamasue, H., Abe, O., Suga, M., Yamada, H., Rogers, M. A., Aoki, S., ... Kasai, K. (2008). Sexlinked neuroanatomical basis of human altruistic cooperativeness. *Cerebral Cortex*, 18, 2331–2340. http://dx.doi.org/10.1093/cercor/bhm254.