Relationship of sensation seeking with the neural correlates of appetitive conditioning

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Abstract

Previous research has linked sensation seeking with a heightened risk for drug abuse and other risk-taking behavior. As appetitive conditioning presents a model for the etiology and maintenance of addictive behavior, investigating sensation seeking in a classical conditioning paradigm might elucidate possible pathways toward addiction within this model. Furthermore, the theoretical concept underlying sensation seeking proposes a negative relationship between reward processing and sensation seeking in only moderately arousing situations, which has been neglected by previous research. This study aimed to investigate this inverse relationship in moderately stimulating situations entailing reward processing using functional magnetic resonance imaging. Subjects (N = 38) participated in a classical conditioning paradigm in which a neutral stimulus (CS+) was repeatedly paired with a monetary reward, while another neutral stimulus (CS−) was not. Imaging results revealed a negative relationship between sensation seeking and neural responses in the insula, amygdala and nucleus accumbens during the early phase and in the dorsal anterior cingulate cortex during the late phase of conditioning. These findings suggest reduced reward learning and consequently diminished processing of outcome expectancy in appetitive conditioning in subjects with high sensation seeking scores. The results are discussed with respect to clinical implications.

Key words: fMRI; reward; classical conditioning; sensation seeking

Introduction

Appetitive conditioning is an important model for the development and maintenance of psychiatric disorders like addictions (Wanigaratne, 2006). Moreover, it can provide insight into how reward learning is altered in personality traits associated with a higher risk of developing these disorders. Investigating the role of individual differences regarding the neural underpinnings of appetitive conditioning might therefore further our understanding of dysfunctional human behavior. In addition, it might offer new approaches for individualized treatments (Lonsdorf & Merz, 2017; Insel & Cuthbert, 2015).

Differential appetitive conditioning paradigms allow for investigating reactions toward an initially neutral stimulus (conditioned stimulus, or CS+) that is repeatedly paired with an appetitive stimulus (unconditioned stimulus, or UCS; e.g. money) compared to a second neutral stimulus (CS−) that is never paired with the UCS. Only few pairings of CS+ and UCS are required to elicit increased responses to the CS+ compared to those to the CS− (conditioned responses, or CRs) (Blechert et al., 2016). CRs may comprise increased valence and arousal ratings, skin conductance responses (SCRs) and blood oxygenation level-dependent (BOLD) responses in the reward network of the brain (Kruse et al., 2017; Klucken et al., 2013). Key brain regions within
the reward network implicated in appetitive conditioning are the amygdala, nucleus accumbens (NAcc), insula, ventral and dorsal anterior cingulate cortex (dACC) and orbitofrontal cortex (OFC) (Martin-Söelch et al., 2007; Haber & Knutson, 2010). While the amygdala is linked to the formation of CS/UCS associations (Balleine et al., 2003; Martin-Söelch et al., 2007; Klucken et al., 2015), the NAcc is considered to play a pivotal role in reward anticipation and temporal difference learning (Spicer et al., 2007; O’Doherty et al., 2002; Tapia León et al., 2018). The insula is associated with the processing of interoceptive information, saliency and its integration with emotional events (Sescousse et al., 2013; Wang et al., 2015; Kurth et al., 2010). While the ventral ACC is ascribed a crucial role in early discriminative learning, the dorsal ACC is assumed to be important for the encoding of the outcomes of a CS+ (Gabriel et al., 2003; Alexander & Brown, 2011; Kruse et al., 2018). Finally, the OFC is thought to be involved in the encoding of expected UCS values (Cox et al., 2005).

Sensation seeking is a personality trait defined by the need for varied, novel and complex sensations and experiences as well as the willingness to take physical and social risks for the sake of such experiences (Zuckerman, 1979, 2016). It is partly well as the willingness to take physical and social risks for the sake of such experiences (Zuckerman, 1979, 2016). It is partly

Materials and methods

Participants

Thirty-eight healthy participants (16 were female, age: M = 23.50 years, s.d. = 3.54 years) were recruited at the University of Giessen. All participants had normal or corrected-to-normal vision, had no current or prior psychiatric or neurological treatment and were right handed. Participants received either course credit or 10€/h in compensation for their time in addition to the monetary reward they won during the experiment. The study complies with the Declaration of Helsinki and was approved by the local ethical review board of the Department of Psychology and Sports Science at the University of Giessen. Written informed consent was obtained from all participants.

Questionnaire

Before the participants entered the scanner, they filled out the German version of the Sensation Seeking Scale V (SSS-V; Beauducel et al., 2003). The total score (M = 22.18, s.d. = 4.55) is comparable to previous normative data (Beauducel et al., 2003).

Experimental procedure

A partial reinforcement appetitive acquisition paradigm as used in Tapia León et al. (2018) consisting of 40 trials was employed. Two isoluminant rectangles in blue and yellow (cross-balanced) served as conditioned stimuli (CS+, CS–). A monetary reward of 50 cents presented on a screen served as the UCS. The reinforcer rate was 50%; thus, half of the CS+ trials were paired with a monetary reward. Unnoticeable to the participants, the acquisition procedure was divided into an early phase (trials 1–20) and a late phase (trials 21–40). Trial sequence was pseudorandomized with the restrictions that (1) the first two trials of each half consisted of a CS+ and a CS– trial, (2) each CS would not be presented more than twice consecutively and (3) each conditioned stimulus (CS+, CS–) was presented in 10 trials of each half to allow for separate analysis of both halves. Participants were instructed regarding CS–UCS contingencies.

Ratings

After the acquisition procedure, participants provided ratings for valence and arousal regarding CS+, CS– and UCS on the nine-point Likert scale of the self-assessment manikin (valence: 1 ‘very unpleasant’ to 9 ‘very pleasant’; arousal: 1 ‘calm and relaxed’ to 9 ‘very aroused’). Differences in the valence and arousal ratings between conditions were examined via paired t-tests (CS+ – CS–) using SPSS 23 (SPSS 23.0 for
Windows, SPSS Inc., Chicago, IL, USA). To test the associations between sensation seeking and differential valence and arousal ratings (CS+ – CS−), one-tailed Pearson’s correlations were performed. Furthermore, correlational analyses were conducted to check for correlations between sensation seeking scores and UCS ratings.

**Skin conductance responses**

SCRs were recorded throughout the experimental procedure and analyzed using Ledalab 3.4.4. (Benedek & Kaernbach, 2010) according to the procedure described in Tapia León et al. (2018). SCR data of three participants had to be discarded due to technical difficulties during data acquisition. Both SCRs and ratings for valence and arousal were measured as indicators of successful conditioning. To examine the relationship between SCRs and sensation seeking, correlational analyses were conducted analogous to the analyses of the ratings.

**fMRI**

Magnetic resonance data were acquired with a 3 T scanner (Magnetom Prisma; Siemens Healthineers, Erlangen, Germany) using a 64-channel head coil. The same scanning parameters, pre-processing pipeline and first-level analysis pipeline were used as described in Tapia León et al. (2018). For the second-level analyses, the CS+ – CS− contrast was investigated separately for the early and the late phases to more clearly discern between the early and late effects of learning, which is consistent with previous studies in the field. Overall, SCR results further indicate successful conditioning. There was no significant correlation between sensation seeking and SCR.

**Results**

**Ratings**

Across participants, higher valence ratings [CS+: M = 6.63, s.d. = 1.63; CS−: M = 3.53, s.d. = 1.75; t(37) = 7.10; P < 0.001] and arousal ratings [CS+: M = 5.79, s.d. = 2.10; CS−: M = 2.66, s.d. = 1.82; t(37) = 6.60; P < 0.001] were revealed for the CS+ than for the CS− (see Figure 1A), showing overall successful conditioning.

**Skin conductance responses**

Repetitive-measures analysis of variance (ANOVA) yielded main effects of CS type [F(1,34) = 9.31; P = 0.004] and time [F(1,34) = 29.83; P < 0.001], which was qualified by a CS type × time interaction [F(1,34) = 4.86; P = 0.034]. A follow-up t-test showed a stronger differential CR in the early phase compared to the late phase of acquisition [t(34) = 2.20; P = 0.034; see Figure 1B]. This pattern is to be expected due to habituation and has been shown in several conditioning studies (Bacigalupo & Luck, 2018; Bulganin et al., 2014; van Ast et al., 2012). Overall, SCR results further indicate successful conditioning. There was no significant correlation between sensation seeking and SCR.

**Correlation of BOLD responses with sensation seeking**

Examining the relationship between sensation seeking and neural correlates of appetitive conditioning, we correlated SSS-V scores with the extracted contrast estimates of the peak voxels of the CS+ – CS− contrast for each ROI for the early and the late phases.

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**Figure 1. Analyses of ratings and SCR.** (A) Differences in mean valence and arousal ratings. (B) Differences in mean SCRs in the early and late acquisition phases. ANOVA yielded the main effects of the CS type and time, qualified by a CS type × time interaction. The error bars represent the SEM. *P < 0.05; **P < 0.01; ***P < 0.001.
phase of acquisition. The analysis showed significant negative correlations as hypothesized, indicating that higher sensation seeking was linked to decreased differential BOLD responses in reward-related brain areas. In the early phase, significant negative correlations in the right NAcc ([6/12/−4]; r = −0.28; P = 0.046), left insula ([−30/26/0]; r = −0.32; P = 0.026) and the right amygdala ([14/−8/−14]; r = −0.29; P = 0.041) were observed (see Figure 2A). In the late phase, analyses showed bilaterally negative correlations between sensation seeking and BOLD responses (CS+ – CS−) in the dACC (left: [−6/24/28]; r = −0.38; P = 0.010; right: [12/16/36]; r = −0.29; P = 0.042; see Figure 2B). The associations remain significant when controlling for valence ratings.

**Discussion**

This study focused on the relationship between the personality trait sensation seeking and the neural correlates of appetitive conditioning in healthy subjects. A classical appetitive conditioning paradigm with colored rectangles as CS and money as a moderately arousing UCS was employed. CRs were found across all subjects in ratings, SCRs and differential BOLD responses to the appetitive CS+ as compared to the CS−. In addition, the differential BOLD response in the amygdala was also negatively associated with sensation seeking. The amygdala is proposed to be crucial for emotional learning, particularly for establishing the link between CS and UCS (Balleine et al., 2003; Martin-Soelch et al., 2007; Klucken et al., 2015). Thus, the negative relationship between sensation seeking and BOLD responses in the amygdala might indicate decreased associative learning in high-sensation seekers compared with low-sensation seekers. Taken together, the correlation of sensation seeking with lower differential responses to the appetitive CS+ as compared to the CS− in the early phase might reflect a reduced formation of CS+–salience in concert with reduced integration of interoceptive signals and CS–UCS association. Furthermore, higher sensation seeking scores were also associated with lower differential arousal ratings (CS+ – CS−). This indicates that subjects with high sensation seeking reported greater differences in arousal. This is in line with our assumption that the absence of risk in moderately stimulating situations leads to a reduced appetitive CS+ – CS− differentiation in individuals with high sensation seeking, as high-sensation seekers report lower differentiation in perceived arousal regarding CS+ and CS−.

In the late phase, sensation seeking is linked with reduced BOLD responses in the dACC, a structure mainly linked with outcome evaluation (Gabriel et al., 2003; Alexander & Brown, 2011; Kruse et al., 2018). This suggests that in the late phase when retrieval of learned associations and outcome evaluation plays a crucial role, high-sensation seekers show reduced processing.
of outcome expectancy toward the appetitive CS+ compared with the CS−. This might be following the reduced differential BOLD responses in brain areas crucial for the formation of differential learning in the early phase. To conclude, we found high-sensation seekers to show an inverse relationship between sensation seeking and reward learning during a classical appetitive conditioning paradigm.

Previous research employed highly stimulating tasks containing risky decision making or stimuli associated with highly arousing situations, in contrast to small amounts of money used as a UCS in the current study. Under those highly stimulating circumstances, high sensation seeking was associated with increased neural activation in these areas (e.g. Abler et al., 2006; Cservenka et al., 2013). This is in line with the concept of an optimal level of stimulation, which suggests that based on the individual trait level of sensation seeking, different levels of stimulation are optimally stimulating (Zuckerman, 2016). Because risky situations are optimally stimulating for high-sensation seekers but less so for low-sensation seekers, these situations reveal positive correlations. In moderately arousing situations, the level of stimulation is more optimal for low-sensation seekers but less so for high-sensation seekers, revealing negative correlations. Thus, our results are in line with the theoretical concept of sensation seeking, demonstrating a modified pattern of reward processing in a moderately stimulating situation compared with previous risk processing paradigms. Indeed, Kruschwitz et al. (2012) found that the neural processing of relatively high rewards and losses differs distinctly from relatively low rewards and losses in the insula and the NAcc. This might be due to the specific trials with relatively low rewards and losses being less stimulating.

Our results are consistent with the RDS theory (Blum et al., 2000), linking high scores of sensation seeking to reward deficiency on a neural level in moderately stimulating contexts. Due to the reward deficiency, individuals might seek out situations more stimulating and thus providing more reward as suggested by previous studies (Abler et al., 2006; Cservenka et al., 2013; Kruschwitz et al., 2012). This is in line with previous research showing that sensation seeking is associated with risk-taking behaviors like substance use and gambling (Zuckerman, 2007). During appetitive conditioning, neutral stimuli become rewarding themselves. Reduced salience processing of conditioned stimuli might effectively reduce the number of stimuli that are perceived as rewarding. Additionally, seeing stimuli associated with reward in everyday life allows us to pursue gaining this reward. Reduced salience processing, as seen in high-sensation seekers, might preclude that, again limiting the number of low risk rewards that appear available in high sensation seeking. This might be a pathway leading high-sensation seekers to seek more stimulating rewards, thus inducing risky behavior.

As a limitation, this study did not vary the degree of arousal the situation entails experimentally. This would seem to be an important next step to further assess the role of sensation seeking in appetitive conditioning. Furthermore, if the separate ROIs were treated as a family of hypotheses, it can be argued that stricter corrections are needed.
As effects of online ratings of the CS might affect the conditioning process, we did not collect any ratings during the acquisition phase. However, as SCR and imaging results reveal different patterns in early and late phases, collecting online ratings might provide helpful insights in future studies.

In addition, future research might further explore the complex interplay of trait sensation seeking, the degree of stimulation the situation comprises and the degree of arousal due to the UCS.

In conclusion, in the present study, we investigated the role of sensation seeking in classical appetitive conditioning. In the early phase of acquisition, sensation seeking was linked to lower differential hemodynamic responses in the NAcc, insula and amygdala, indicating reduced reward processing and learning. In the late phase, sensation seeking was negatively associated with differential activation in the dACC, indicating reduced retrieval of outcome expectancy. This highlights the importance of the individual level of optimal stimulation for appetitive conditioning.

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**Conflicts of interest**

None declared.

**References**

Abler, B., Walter, H., Erk, S., Kammerer, H., Spitzer, M. (2006). Prediction error as a linear function of reward probability is coded in human nucleus accumbens. *Neuromage*, 31, 790–95. doi:10.1016/j.neuroimage.2006.01.001.

Alexander, W.H., Brown, J.W. (2011). Medial prefrontal cortex as an outcome-anticipator predictor. *Nature Neuroscience*, 14, 1338–44. doi:10.1038/nn.2921.

Bacigalupo, F., Luck, S.J. (2018). Event-related potential components as measures of aversive conditioning in humans. *Psychophysiology*, 55, 1–12. doi:10.1111/psyp.13015.

Balleine, B.W., Killcross, A.S., Dickinson, A. (2003). The effect of lesions of the basolateral amygdala on instrumental conditioning. *The Journal of Neuroscience*, 23, 666–70. doi:10.1523/JNEUROSCI.02-02-2003.

Beauducel, A., Strobel, A., Brocke, B. (2003). Psychometrische Eigenschaften und Normen einer deutschsprachigen Fassung der Sensation Seeking-Skalen, Form V. *Diagnostica*, 49, 61–72. doi:10.1026/0012-1924.49.2.61.

Benedek, M., Kaerbach, C. (2010). A continuous measure of phasic electrodermal activity. *Journal of Neuroscience Methods*, 190, 80–91. doi:10.1016/j.jneumeth.2010.04.028.

Biebert, J., Testa, G., Georgii, C., Klimesch, W., Wilhelm, F.H. (2016). The Pavlovian craver: neural and experiential correlates of single trial naturalistic food conditioning in humans. *Physiology & Behavior*, 158, 18–25. doi:10.1016/j.physbeh.2016.02.028.

Blum, K., Braverman, E.R., Holder, J.M., et al. (2000). Reward deficiency syndrome. A biogenetic model for the diagnosis and treatment of impulsive, addictive, and compulsive behaviors. *Journal of Psychoactive Drugs*, 32(Suppl. i-iv), 1–112. doi:10.1080/02791072.2000.10736099.

Büchel, C., Peters, J., Banaschewski, T., et al. (2017). Blunted ventral striatal responses to anticipated rewards foreshadow problematic drug use in novelty-seeking adolescents. *Nature Communications*, 8, 14140. doi:10.1038/ncomms14140.

Bulganin, L., Bach, D.R., Wittmann, B.C. (2014). Prior fear conditioning and reward learning interact in fear and reward networks. *Frontiers in Behavioral Neuroscience*, 8, 67. doi:10.3389/fnbeh.2014.00067.

Cox, S.M.L., Andrade, A., Johnsrude, I.S. (2005). Learning to like: a role for human orbitofrontal cortex in conditioned reward. *The Journal of Neuroscience*, 25, 2733–40. doi:10.1523/JNEUROSCI.3360-04.2005.

Cservenka, A., Hertzing, M.M., Seghete, K.L.M., Hudson, K.A., Nagel, B.J. (2013). High and low sensation seeking adolescents show distinct patterns of brain activity during reward processing. *Neuromage*, 66, 186–93. doi:10.1016/j.neuroimage.2012.11.003.

Dillon, D.G., Holmes, A.J., Jahn, A.L., Bogdan, R., Wald, L.L., Pizzagalli, D.A. (2008). Dissociation of neural regions associated with anticipatory versus consummatory phases of incentive processing. *Psychophysiology*, 45, 36–49. doi:10.1111/j.1469-8986.2007.00594.x.

Gabriel, M., Burbans, L., Kasche, A. (2003). Consideration of a unified model of amygdalar associative functions. *Annals of the New York Academy of Sciences*, 985, 206–17. doi:10.1111/j.1749-6632.2003.tb07083.x.

Haber, S.N., Knutson, B. (2010). The reward circuit. Linking primate anatomy and human imaging. *Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology*, 35, 4–26. doi:10.1038/npp.2009.129.

Hebb, D.O. (1955). Drives and the C. N. S. (conceptual nervous system). *Psychological Review*, 62, 243–54. doi:10.1037/h0041823.

Hommer, D.W., Bjork, J.M., Gilman, J.M. (2011). Imaging brain response to reward in addictive disorders. *Annals of the New York Academy of Sciences*, 1216, 50–61. doi:10.1111/j.1749-6630.2010.05889.x.

Insel, T.R., Cuthbert, B.N. (2015). Medicine. Brain disorders? Precisely. *Science (New York, N.Y)*, 348, 499–500. doi:10.1126/science.aab2358.

Joseph, J.E., Liu, X., Jiang, Y., Lynam, D., Kelly, T.H. (2009). Neural correlates of emotional reactivity in sensation seeking. *Psychological Science*, 20, 215–23. doi:10.1111/j.1467-9280.2009.02283.x.

Klucken, T., Kruse, O., Wehrum-Osinsky, S., Hennig, J., Schweckendiek, J., Stark, R. (2015). Impact of COMT Val158Met-polymorphism on appetitive conditioning and amygdala/prefrontal effective connectivity. *Human Brain Mapping*, 36, 1093–101. doi:10.1002/hbm.22688.

Kruck, T., Wehrum, S., Schweckendiek, J., et al. (2013). The 5-HTTLPR polymorphism is associated with altered hemodynamic responses during appetitive conditioning. *Human Brain Mapping*, 34, 2549–60. doi:10.1002/hbm.22085.

Kruschwitz, J.D., Simmons, A.N., Flagan, T., Paulus, M.P. (2012). Nothing to lose: processing blindness to potential losses drives thrill and adventure seekers. *Neuromage*, 59, 2850–59. doi:10.1016/j.neuroimage.2011.09.048.

Kruse, O., Tapia León, I., Stalder, T., Stark, R., Klucken, T. (2018). Altered reward learning and hippocampal connectivity following psychosocial stress. *Neuromage*, 15–25. doi:10.1016/j.neuroimage.2017.12.076.

Kruse, O., Tapia León, I., Stark, R., Klucken, T. (2017). Neural correlates of appetitive extinction in humans. *Social Cognitive and Affective Neuroscience*, 12, 106–15. doi:10.1093/socan/snw157.

Kurth, F., Zilles, K., Fox, P.T., Laird, A.R., Eickhoff, S.B. (2010). A link between the systems. Functional differentiation and integration within the human insula revealed by...
meta-analysis. Brain Structure & Function, 214, 519–34. doi: 10.1007/s00429-010-0255-z.

LaBar, K.S., Gatenby, J.C., Gore, J.C., LeDoux, J.E., Phelps, E.A. (1998). Human amygdala activation during conditioned fear acquisition and extinction: a mixed-trial fMRI study. Neuron, 20(5), 937–45 doi:10.1016/S0896-6273(00)80475-4.

Lindsley, D.B. (1961). The reticular activation system. In: Sheer, D.E., editor. Electrical Stimulation of the Brain, Austin: The University of Texas Press, pp. 331–49.

Lonsdorf, T.B., Menz, M.M., Andreatta, M., Fullana, M.A., Golkar, A., Haaker, J., et al. (2017). Don’t feel fear ‘feeling condition’: Methodological considerations for the design and analysis of studies on human fear acquisition, extinction, and return of fear. Neuroscience and Biobehavioral Reviews, doi:10.1016/j.neubiorev.2017.02.026.

Lonsdorf, T.B., Merz, C.J. (2017). More than just noise. Individual differences in fear acquisition, extinction and return of fear in humans—biological, experiential, temperamental factors, and methodological pitfalls. Neuroscience and Biobehavioral Reviews, 80, 703–28. doi: 10.1016/j.neubiorev.2017.07.007.

Luijten, M., Schellekens, A.F., Kühn, S., Machielse, M.W.J., Sescousse, G. (2017). Disruption of reward processing in addiction. An image-based meta-analysis of functional magnetic resonance imaging studies. JAMA Psychiatry, 74, 387–98. doi:10.1001/jamapsychiatry.2016.3084.

Martin-Soechl, C., Linthicum, J., Ernst, M. (2007). Appetitive conditioning: neural bases and implications for psychopathology. Neuroscience and Biobehavioral Reviews, 31, 426–40. doi:10.1016/j.neubiorev.2006.11.002.

Milad, M.R., Wright, C.I., Orr, S.P., Pitman, R.K., Quirk, G.J., Rauch, S.L. (2007). Recall of fear extinction in humans activates the ventromedial prefrontal cortex and hippocampus in concert. Biological Psychiatry, 62(5), 446–54 doi:10.1016/j.biopsycho.2006.10.011.

Norbury, A., Husain, M. (2015). Sensation-seeking dopaminergic modulation and risk for psychopathology. Behavioural Brain Research, 288, 79–93. doi:10.1016/j.brbr.2015.04.015.

O’Doherty, J.P., Deichmann, R., Critchley, H.D., Dolan, R.J. (2002). Neural responses during anticipation of a primary taste reward. Neuron, 33, 815–26. doi:10.1016/S0896-6273(02)00603-7.

O’Doherty, J.P., Buchanan, T.W., Seymour, B., Dolan, R.J. (2006). Predictive neural coding of reward preference involves dissociable responses in human ventral midbrain and ventral striatum. Neuron, 49, 157–66. doi:10.1016/j.neuron.2005.11.014.

Phelps, E.A., Delgado, M.R., Nearing, K.I., LeDoux, J.E. (2004). Extinction learning in humans: role of the amygdala and vmPFC. Neuron, 43(6), 897–905 doi:10.1016/j.neuron.2004.08.042.

Rademacher, L., Krach, S., Kohls, G., Irmak, A., Grunder, G., Spreckelmeyer, K.N. (2010). Dissociation of neural networks for anticipation and consumption of monetary and social rewards. NeuroImage, 49, 3276–85. doi:10.1016/j.neuroimage.2009.11.089.

Sescousse, G., Caldú, X., Segura, B., Dreher, J.-C. (2013). Processing of primary and secondary rewards. A quantitative meta-analysis and review of human functional neuroimaging studies. Neuroscience and Biobehavioral Reviews, 37, 681–96. doi:10.1016/j.neubiorev.2013.02.002.

Spicer, J., Galvan, A., Hare, T.A., Voss, H., Glover, G., Casey, B. (2007). Sensitivity of the nucleus accumbens to violations in expectation of reward. NeuroImage, 34, 455–61. doi:10.1016/j.neuroimage.2006.09.012.

Tapia León, I., Kruse, O., Stalder, T., Stark, R., Klucken, T. (2018). Neural correlates of subjective CS/UCS association in appetitive conditioning. Human Brain Mapping, 1637–47. doi:10.1002/hbm.23940.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., et al. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. NeuroImage, 15, 273–89. doi:10.1006/nimg.2001.0978.

van Ast, V.A., Vervliet, B., Kindt, M. (2012). Contextual control over expression of fear is affected by cortisol. Frontiers in Behavioral Neuroscience, 6, 67. doi:10.3389/fnbeh.2012.00067.

Walter, B., Blecker, C., Kirsch, P., Sammer, G., Schienle, A., Stark, V., Vaitl, D. (2003). MARINA: An easy to use tool for the creation of masks for region of interest analyses. [CD-ROM]. NeuroImage, 19.

Wang, L., Yu, H., Hu, J., et al. (2015). Reward breaks through center-surround inhibition via anterior insula. Human Brain Mapping, 36, 5233–51. doi:10.1002/hbm.23004.

Wanigaratne, S. (2006). Psychology of addiction. Psychiatry, 5, 455–460. doi:10.1053/j.mppsy.2006.09.007.

Wundt, W.M. (1893). Grundzüge der Physiologischen Psychologie, Leipzig: Engelman.

Zheng, Y., Liu, X. (2015). Blunted neural responses to monetary and social rewards. Human Brain Mapping, 36, 5233–51. doi:10.1002/hbm.23004.

Zuckerman, M. (1979). Sensation Seeking: Beyond the Optimal Level of Arousal, Hillsdale, NJ: Erlbaum.

Zuckerman, M. (2007). Sensation Seeking and Risky Behavior, Washington: American Psychological Association.

Zuckerman, M. (2016). Sensation Seeking: Beyond the Optimal Level of Arousal, Hove: Taylor & Francis Group.