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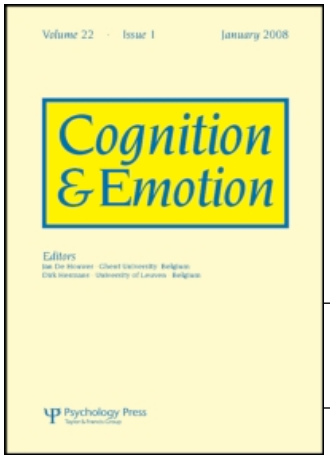

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Modulation of cognitive flexibility by hunger and desire

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Modulation of cognitive flexibility by hunger and desire

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Knowing when to persevere with a plan and knowing when to ditch it and change strategy is highly adaptive and breaks down in several frontal and striatal disorders. Cognitive flexibility is also susceptible to tonic influences of neuromodulators (such as dopamine) and so may be influenced by everyday fluctuations in processes known to depend upon them (such as motivation). The current study employed an attentional shifting paradigm to examine the influence of changes in food-related motivational state in healthy volunteers. Hunger was induced through fasting (physiological manipulation) or through the presentation of appetitive food cues prior to testing (desire manipulation). The desire manipulation produced a stronger effect than fasting by inducing errors when participants were attempting to shift. The results suggest that everyday fluctuations in appetite and desire can produce a significant impact on cognition, highlighting implications for our understanding of excessive motivational control including maladaptive eating behaviour.

INTRODUCTION

The complex environment we live in requires the maintenance of a consistent response pattern to certain conditions but also the ability to adapt when conditions change. This demand for both consistency and adaptation is reflected by cognitive processing systems that monitor and finely tune behaviour in order to achieve goals (Cools & Robbins, 2004). The prefrontal cortex (PFC), along with its associated striatal circuitry, is thought to play an important role in such monitoring, maintenance and flexibility (Miller & Cohen, 2001). Cognition and behaviour should also be modulated by external and internal environmental variables, such as hunger and the

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availability of food. So, for example, an increase in hunger brought about by fasting should bias attention and behaviour towards food-related stimuli and foraging, whereas foraging should be trumped, in attentional and behavioural terms, by imminent threat and predation. To date, little work has examined the interface between food-related motivational variables and cognitive flexibility (Morris & Dolan, 2001).

Cognitive flexibility can be captured by performance on tasks that contrast different kinds of attentional shifting such as the WCST and its analogues (Owen et al., 1992; Roberts, Robbins, Everitt, & Muir, 1992). A typical task consists of a solution search during which attention has to be transferred from one perceptual dimension to another, following a rule, in order to identify a target stimulus from one of the perceptual dimensions (for example, houses vs. faces). This task requires a combination of consistency, once a target has correctly been identified, and flexibility, in identifying a new target once the old one is no longer correct. Intradimensional shifts (IDs) are those where the participant continues to search for targets within the same dimension (continuing to pursue houses), whereas, if the participant chooses to change dimension (switching from houses to faces), then they make an extradimensional (ED) shift. These two types of shift are conceptually (and potentially neurobiologically) separable—foraging for food requires a complex balance between dimensional maintenance and shifting.

Hunger plays a central role in energy regulation and affects behaviour by eliciting food seeking and contributing to the initiation of feeding. Since food acquisition success partly depends on elaborate strategic behaviours, one would expect adjustments of the cognitive system to hunger to be adaptive. Further, set-shifting processes depend upon corticostriatal circuitry (Chudasama & Robbins, 2006; Rogers, Andrews, Grasby, Brooks, & Robbins, 2000), re-entrant loops between areas in the prefrontal cortex and the basal ganglia (Alexander, Delong, & Strick, 1986).

One might therefore hypothesise that state-dependent manipulations of hunger should produce a modulatory influence over cognitive processing, and in particular set-shifting, by reducing the tendency to make ED shifts. The mesolimbic dopamine (DA) system, providing a modulatory input to corticostriatal circuitry, has been widely implicated in stimulus-induced motivational arousal and so a more specific hypothesis is that hunger, induced not by food deprivation, but by the presentation of food-associated appetitive stimuli should also modulate set-shifting behaviour. Therefore, in the current study, healthy volunteers completed a set-shifting task (the set-shifting task itself did not involve food-associated stimuli; the visual category dimensions were pictures of faces or houses) while they were either hungry or sated (physiological manipulation) and after being exposed to either appetitive food cues, or control (flower) stimuli (desire manipulation).

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The specific task to assay cognitive flexibility was chosen for several reasons: critically, the task allows identification of the exact target that participants have chosen and this enables categorisation of specific shifting behaviour and error type (e.g., ED vs. ID shifts); it uses non-novel dimensions, and manipulations to reduce the impact of learned irrelevance; the use of partial feedback also equates experienced reward contingencies for both ID and ED shifts. Thus ID- and ED-shifting behaviour is cleaner in terms of task processing and also for subsequent experimental analysis. It is also worth noting that this specific task has been shown to activate ventrolateral PFC and anterior cingulate in ED shifting, two areas that are also implicated in affective influences over cognition (Hampshire & Owen, 2006).

METHOD

Participants

Sixteen students (9 female) participated in the experiment as part of their course credit. For the hungry condition, they were instructed to not eat for 5 hours prior to the experiment. The study was approved by Local Research Ethics Committee.

Design

The two participant-related within-subject factors were State (Physiological: hungry vs. sated) and Desire (Stimulus-induced: food vs. nonfood) and their effect was assessed on various measures of attentional set-shifting including the number of ID and ED shifts, as well as associated errors and reaction times. Measures of self-reported hunger were also recorded.

Procedure

Set-shifting tasks are commonly derived from traditional rule-learning paradigms such as the Wisconsin card-sorting task; in essence, the participant's role was to identify a target stimulus from an array of four exemplars, which themselves came from two categories (faces and buildings; Hampshire & Owen, 2006, Figure 1, p. 1681). Each array of stimuli was presented as two superimposed pairs presented on either side of a computer screen. So, on each side of the screen were a building stimulus and a face stimulus (the transparency of the stimuli were set such that both stimuli were visible and identifiable). On each trial, the participants were required to indicate using the keyboard on which side of the screen they thought the target was located. Participants made a response to indicate which side of the screen they believed the correct stimulus to be. Following a response, the stimuli disappeared from the screen, prior to a new trial commencing.

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Feedback was provided on every second response ("correct" or "incorrect" was presented on the screen for 0.6 s, indicating whether the two preceding stimuli they had chosen were both the target or not). Each trial consisted of a different combination of the face and building stimuli (though always one face and one building per compound).

After 6 correct responses to the target (i.e., 3 positive feedback events), a change of target occurred. The change was either a new target of the same dimension (requiring an intradimensional shift) or a new target in the other dimension (requiring an extradimensional shift). The new target could also be in the form of a stimulus group change, in which new compound-stimulus pairs were presented (i.e., a novel set of house and face stimuli were introduced), or simply in the form of a rule change, in which the group would stay the same and a previous nontarget would become the target (i.e., the existing house and face compounds were retained, but the specific target stimulus was changed). Participants were clearly instructed to keep responding to the correct target until informed that it was no longer the target and to respond "as quickly and accurately as possible". The task duration was 8 minutes. The crucial cognitive process we were interested in was the participants' shift of their responding to a different category (ED shift), or to a different item in the same category (ID shift). This design was adopted primarily to allow participants to dictate the pace of events and to determine for themselves the number of shifts to make during their time on task—an important consideration given our hypothesised effect of motivational manipulations on the tendency to initiate shifting behaviour. Secondarily, the design was based on previous work (Hampshire & Owen, 2006) in order to allow comparison of results and to prepare for future exploration of these manipulations within a neuroimaging context.

During task performance, the participant could shift their responding to a new target at any time (though this was most likely following feedback of an incorrect response). As the computer tracked the stimulus that the participant had previously responded to, it was possible to determine how often they made an ID shift (changing targets within the same dimension e.g., one face to the other face) and how often they made an ED shift (e.g., changing from a face to a building). Thus it was possible to calculate differences in the tendency to make correct and incorrect ID and ED shifts across the task. For the analysis, as well as calculating the number of correct shifts that a participant made, we also counted the *number of errors* committed when the participant shifted their responding to a new target in either the same (ID) or the alternate dimension (ED): after each change, the number of responses before finding the correct target was counted. In some trials the participant first found and then lost the new target before reaching criterion (6 correct responses). These incorrect responses were counted as errors in completing the switch. Thus we could analyse the total

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number of errors made on the task, as well as the ratio of ED and ID errors. To achieve the latter, an index of cognitive inflexibility, we calculated the ratio of ED errors committed to total errors committed (the sum of ED and ID). This is referred to as the Inflexibility Ratio (IR); a higher number reflecting a greater proportion of responses taken to shift across categories (ED) than within (ID). Importantly, this reflects the ratio of errors made when an individual chose to make either an ED or ID shift, independently of whether the correct target actually changed.

Participants came to the laboratory on two consecutive days, once for the hungry and once for the sated condition. The sessions were identical, with half the participants starting with the hungry one. During each session the participants completed two equivalent versions of the set-shifting task and watched a presentation (induction procedure) prior to each run of set-shifting. The desire-induction presentation consisted of 50 pictures of food (4 s each, 1 s interval) and participants were asked to imagine what the food would taste like when eaten. In the control condition, the pictures depicted flower arrangements (nonfood) and the participants were asked to imagine what it would be like to buy the flowers. The sequence of the presentations was counterbalanced.

After the first presentation, participants completed the attentional shifting task. Then the participants viewed the other set of pictures (food or nonfood), again followed by the task. At the beginning of each session and after each component of the experiment, the participants completed a short self-report questionnaire that included scales of happiness, arousal, hunger, and fullness.

RESULTS

State manipulation

Immediately after the induction procedure, participants reported how hungry they were. Using those scores, we carried out a 2×2 repeated-measures analysis of variance (ANOVA) with the factors State (hungry, sated), and Desire (food, nonfood: presentation of food items and flower arrangements, respectively). The first factor represents physiological, deprivation-induced hunger for food, and the second stimulus-induced desire for it. The ANOVA revealed two main effects but no interaction, $F(1, 15) = 0.494$, $MSE = 36$, showing that participants indeed indicated themselves more hunger during the hungry than during the sated session, $F(1, 15) = 22.77$, $MSE = 22{,}201$, $p < .001$. They also indicated more hunger after exposure to food stimuli than after exposure to nonfood stimuli, $F(1, 15) = 7.56$, $MSE = 1463$, $p < .05$.

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To specifically evaluate the impact of the food pictures on stimulus-induced desire, we compared hunger scores before and after the induction procedures (prior to shifting task). There was a large significant increase in hunger for the food presentation, $t(15) = 4.75$, $p < .001$, while the change after the presentation of nonfood was not different from zero, $t(15) = 1.03$, $p = .32$.

Set-shifting performance

In the attentional shifting task, the average number of targets identified by the participants was 67 ($SD = 14.1$; range = 40–86). Since the task was time limited, the total number of each type of event varied between individuals, the averages were 81 ED shifts and 57 ID shifts. The number and type of shifts did not differ across the conditions (Fs < 2).

In the next step, we calculated the number of ID and ED errors participants committed, which allowed us to analyse the total number of errors made on the task, as well as the ratio of ED and ID errors, the Inflexibility Ratio (IR). As can be seen in Figure 1 the manipulations of State and Desire did influence the number of errors made when making ID and ED shifts. Broadly speaking those conditions that produced an increase in self-reported hunger appeared also to produce a greater number of errors, with ED shifts appearing more sensitive to errors than ID shifts.

Initially, we conducted an analysis of the total number of errors committed using a 2×2 ANOVA with the factors State (hungry/sated)

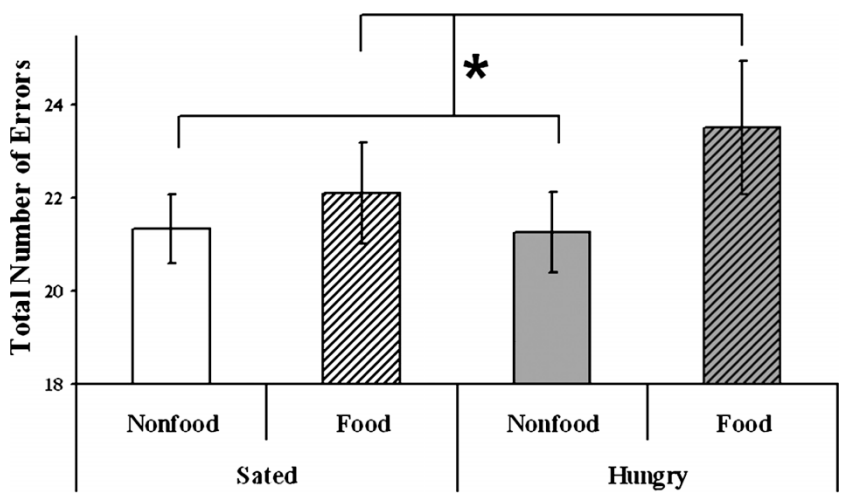

Figure 1. Mean total number of errors committed in all conditions. The presentation of food items increased the total number of errors, but fasting alone had no impact. Error bars indicate the standard error. $^*p < .05$.

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and Desire (nonfood/food). The ANOVA indicated no difference between the sated and hungry State as such, $F(1, 14) = 0.69$, $MSE = 30.10$, but a higher number of errors after viewing food pictures, i.e., a main effect of Desire, $F(1, 15) = 5.72$, $MSE = 162.36$, $p < .05$, an effect that seems particularly pronounced in the Hungry-Food condition (Figure 1). In general, the aroused motivational state induced by the presentation of food cues impaired shifting behaviour as measured by total errors during shifts.

To explore the types of error made, a 2×2 repeated-measures ANOVA of the IR was performed with the factors State (hungry/sated), and Desire (food/nonfood). The ANOVA revealed a State × Desire interaction, $F(1, 15) = 6.36$, $MSE = 0.01$, $p < .05$ (Figure 2a), reflecting higher IR scores in conditions Sated-Food and Hungry-Nonfood than for Sated-Nonfood and Hungry-Food. This suggests that a single "hunger" manipulation (be it hunger or food) increases the ratio of ED to ID errors. Surprisingly, ratios were very similar after either Sated alone (without a presentation of food pictures) or with both hunger and food induction together. A plot of the total numbers of both ID and ED errors (Figure 2b) reveals that the decreased IR in the Hungry-Food condition does not reflect a decrease of ED errors, but an increase in ID errors. This was confirmed by a $2 \times 2 \times 2$ ANOVA with the factors State (hungry/sated), Desire (food/nonfood) and Shift (ID/ED) revealing a three-way interaction, $F(1, 15) = 6.45$, $MSE = 15.47$, $p < .05$, as well as two main effects: Induction, $F(1, 15) = 5.23$, $MSE = 18.23$, $p < .05$, reflected as increased overall errors following food presentations; and Shift, $F(1, 15) = 7.22$, $MSE = 18.99$, $p < .05$, reflecting increased errors during ED shifts, relative to ID shifts. While the factor of Gender produced no significant effects or trends on task performance, the analysis of Order produced a trend towards an Order × Desire interaction, $F(1, 14) = 3.96$, $MSE = 11.45$, $p = .07$. The presentation of food stimuli (desire manipulation) prior to set-shifting induced a numerically greater number of errors irrespective of Order (whether a participant saw food images or flower images first) though this was primarily driven in the food-first Order. (No other analyses including gender and order as factors revealed any effects of interest, Fs < 2.)

Next, the analysis focused on response times during shifting. Each time when the participant shifted target to either the same (ID) or the opposite dimension (ED), the respective time was measured. A $2 \times 2 \times 2$ repeated-measures ANOVA was performed with the factors State (hungry/sated), Desire (nonfood/food), and Shifts (ID/ED). It revealed only a State × Shifts interaction, $F(1, 15) = 20.87$, $MSE = 676{,}430$, $p < .001$ (all other Fs < 2), suggesting that response time difference between ID and ED responses is not equal for the sated and hungry states. Exploration of simple-interaction effects using follow-up ANOVAs revealed that ED responses were slower

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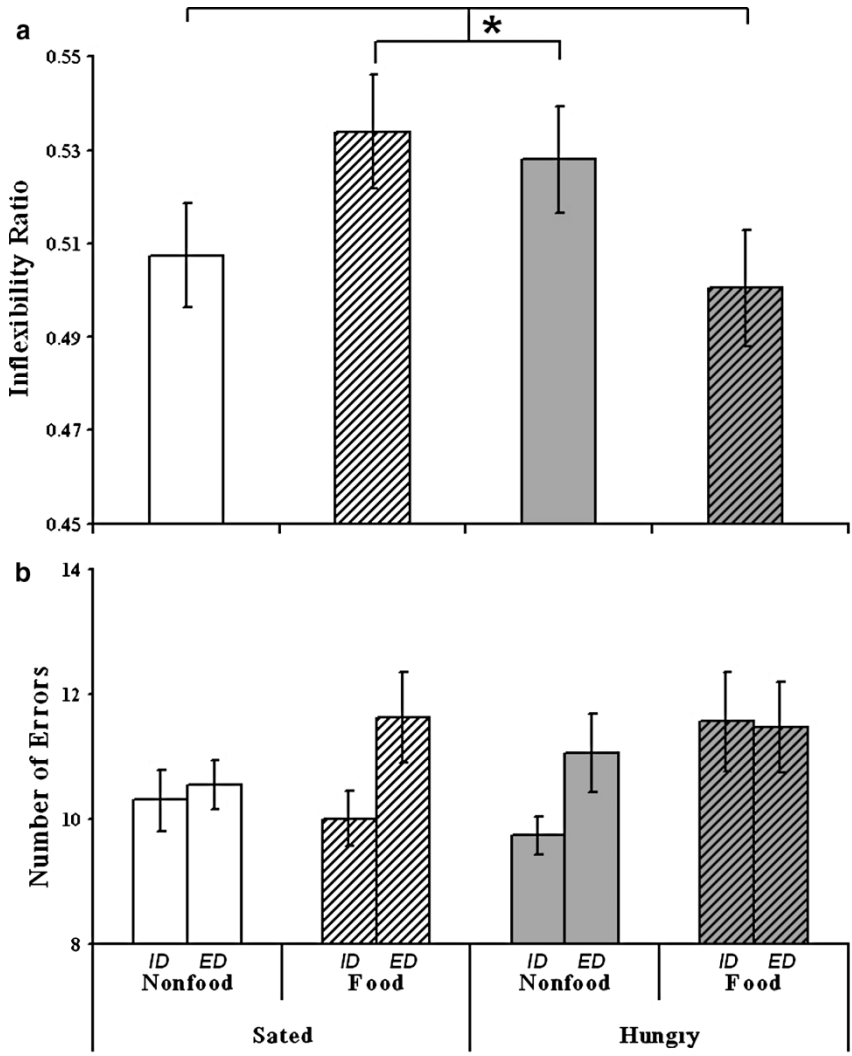

Figure 2. Errors committed in the shifting task. (**a**) Mean inflexibility ratio (IR; calculated as ED errors/ED+ID errors) for all conditions. Inflexibility is higher for Sated-Food and Hungry-Nonfood than for Sated-Nonfood and Hungry-Food conditions. (**b**) Mean number of ID and ED errors committed in all conditions. Error bars indicate the standard error. $^*p < .05$.

than ID when participants were Sated (ID: 1.20 s, $SD = 0.16$; ED: 1.45 s, $SD = 0.35$) $F(1, 15) = 17.87$, $MSE = 477{,}020$, $p < .001$, but that there was no speed difference when participants were hungry (ID: 1.43 s, $SD = 0.48$; ED: 1.39 s, $SD = 0.38$) $F(1, 15) = 0.48$, $MSE = 17{,}298$. This suggests that the State and Induction elicited changes in error rates is not a consequence of

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increased response speed and instead suggests that increased hunger appears to slow response times, perhaps towards a ceiling reflected in ED reaction times.

DISCUSSION

This study shows that cognitive flexibility as assessed by set-shifting performance is susceptible to subtle changes in motivational state that can, and do, occur in our everyday lives (as opposed to cognitive effects induced by extreme states like hypo- and hyperglycaemia). Asking participants to fast for 5 hours prior to testing significantly increased self-reported hunger, as did presenting participants with a 4-minute slideshow of food-related cues and asking them to think about the stimuli presented. Such changes in perceived hunger state did not have the hypothesised impact on a participants' tendency to initiate shifting strategies, as measured by the overall number and type (ID vs. ED) of shifts made by participants on the present task. However, the interaction of fasting and cue-induction, did have an impact on the number of errors made by participants while shifting, and also on their reaction time to initiate shifts. Induction of desire by food-related cues alone, produced a significant increase in total errors on the task. Further, comparison of error data for ID and ED shifts, suggests that ED-shifting is initially more sensitive to disruption by motivational manipulations, howsoever induced, and that ID errors appear as hunger becomes more pronounced—in the current study, in the condition combining *both* forms of appetite induction (fasting and cue-induction). Finally, response time data suggest that impairments in shifting are not the result of a speed–accuracy trade-off and instead may reflect a gross increase in distractibility induced by hunger, or, alternatively, a more subtle modulation of cognitive flexibility by state induction.

Hunger and cognition

Only a few studies have explored the relationship between appetite and cognition. For example, fasting-induced hunger during learning has been demonstrated to improve long-term memory for food-related cues (Morris & Dolan, 2001). It has also been shown that fasting produces attentional biases towards food cues, using variants of the Stroop task or with the dot-probe task, and that these biases appear to relate to participants' self-reported hunger levels (Green, Elliman, & Rogers, 1996; Mogg, Bradley, Hyare, & Lee, 1998). It is worth emphasising that in the present study the greatest effects on cognition were observed, not following fasting, but following the manipulation that we have described as stimulus-induced desire—there are

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clear implications for this finding to society with its ubiquitous prevalence and availability of food and food-stimuli.

The relationship between hunger and errors during set-shifting suggests that ED shifts, the ability to disengage current strategies and apply new ones, are more susceptible to state manipulations. One reason for this may be that when either of the hunger manipulations was employed alone it focused cognition on the current target dimension resulting in a greater number and proportion of ED shifting errors (and a slight tendency to reduced ID errors). When the motivational manipulations were combined the participants may have lost their top down structure in the solution search and began to have trouble with cognitive flexibility in general. While these error data are broadly consistent with the hypothesis that motivation should impact upon cognition, the current results did not show a change in the tendency of participants to initiate ID or ED shifts following changes in hunger. However, the current cognitive task did not employ food-related dimensions or targets, and so it is possible that selective effects of hunger on shifting strategies may require food stimuli to be present as targets (or distractors) of behaviour. Therefore, hunger state may produce a gross impact upon cognitive performance in general, as evidenced by increased error rates during shifts in the current task, and may be hypothesised to have more selective effects on cognitive flexibility when task-related parameters are motivationally salient; a domain for future exploration and an interesting neurobiological challenge for the brain in determining the motivational salience and congruence of environmental stimuli.

The neurobiology of motivation–cognition interactions

Previous fMRI analysis of the task used in the current study has demonstrated activity in ventrolateral prefrontal cortex and anterior cingulate cortex during ED shifting—both areas implicated in affective influences over cognition and also cortical afferents to striatal circuitry. Indeed, attentional set-shifting is believed to be dependent upon corticostriatal circuitry (Chudasama & Robbins, 2006; Crofts et al., 2001; Hampshire & Owen, 2006; Rogers et al., 2000).

Dopamine (DA), and in particular the *mesolimbic* pathway innervating the ventral striatum, is a core component of the brain's motivational arousal system: food-associated stimuli produce increased DA in the ventral striatum of animals and humans, while damage to the ventral striatum, or disruption of its DA-ergic innervation abolishes motivational arousal for food, sex and drugs (Everitt et al., 1999; Parkinson et al., 2002; Volkow et al., 2002). DA is also implicated in cognitive flexibility; so, for example, DA antagonists impair set-shifting in humans and rats (Floresco, Magyar, Ghods-Sharifi, Vexelman, & Tse, 2006; Mehta, Manes, Magnolfi, Sahakian, & Robbins,

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2004), DA medication recovers shifting deficits in Parkinson's patients (Cools, Barker, Sahakian, & Robbins, 2001) and specific deficits in ED shifting, including perseveration, are thought to be due to dysfunction in the DA-ergic innervation of PFC-caudate interactions (Chudasama & Robbins, 2006). Therefore, a mechanism by which motivation and cognition can interface is via DA *across* corticostriatal circuits (Haber, Fudge, & McFarland, 2000; Parkinson, Cardinal, & Everitt, 2000). In this case, arousal and desire induced by food cues trigger DA release in the mesolimbic system, which would in turn modulate the DA-ergic innervation of the mesocortical and nigrostriatal system resulting in a change in the balance of set-shifting behaviour (Haber et al., 2000).

Conclusion

Cognitive flexibility has been shown to differ across individuals (Wager, Jonides, & Smith, 2006), is affected in neuropsychological disorders (Owen et al., 1993), and has been shown to change as a result of exogenous manipulations of neurotransmitters such as dopamine and serotonin (Ornstein et al., 2000; Rogers et al., 1999; Rogers & Robbins, 2001). The current study adds to this data set by demonstrating that changes in motivational state can also produce significant changes in set-shifting behaviour.

There are several important implications of this study: first, it demonstrates a psychological interface between motivation and cognition; second it implicates corticostriatal circuitry, and in particular interactions between ventral striatal and caudate components, in this motivation–cognition interface; third, it reinforces the contention that cognitive performance is sensitive to everyday fluctuations in motivational state; finally, it demonstrates that passive presentation of food cues can produce a greater impact on cognition than fasting—as such, the cognitive impact of food-related stimuli, ubiquitous in our society, represents an important avenue for further research.

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REFERENCES

Alexander, G. E., Delong, M. R., & Strick, P. L. (1986). Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annual Review of Neuroscience*, *9*, 357–381.

Downloaded By: [University of Wales Bangor] At: 08:41 22 May 2008

Chudasama, Y., & Robbins, T. W. (2006). Functions of frontostriatal systems in cognition: Comparative neuropsychopharmacological studies in rats, monkeys and humans. *Biological Psychology*, *73*(1), 19–38.

Cools, R., Barker, R. A., Sahakian, B. J., & Robbins, T. W. (2001). Enhanced or impaired cognitive function in Parkinson's disease as a function of dopaminergic medication and task demands. *Cerebral Cortex*, *11*(12), 1136–1143.

Cools, R., & Robbins, T. W. (2004). Chemistry of the adaptive mind. *Philosophical Transactions of the Royal Society A: Mathematical, Physical, and Engineering Sciences*, *362*(1825), 2871–2888.

Crofts, H. S., Dalley, J. W., Collins, P., Van Denderen, J. C., Everitt, B. J., Robbins, T. W., et al. (2001). Differential effects of 6-OHDA lesions of the frontal cortex and caudate nucleus on the ability to acquire an attentional set. *Cerebral Cortex*, *11*(11), 1015–1026.

Everitt, B. J., Parkinson, J. A., Olmstead, M. C., Arroyo, M., Robledo, P., & Robbins, T. W. (1999). Associative processes in addiction and reward. The role of amygdala-ventral striatal subsystems. *Annals of the New York Academy of Sciences*, *877*, 412–438.

Floresco, S. B., Magyar, O., Ghods-Sharifi, S., Vexelman, C., & Tse, M. T. (2006). Multiple dopamine receptor subtypes in the medial prefrontal cortex of the rat regulate set-shifting. *Neuropsychopharmacology*, *31*(2), 297–309.

Green, M. W., Elliman, N. A., & Rogers, P. J. (1996). Hunger, caloric preloading and the selective processing of food and body shape words. *British Journal of Clinical Psychology*, *35*(1), 143–151.

Haber, S. N., Fudge, J. L., & McFarland, N. R. (2000). Striatonigrostriatal pathways in primates form an ascending spiral from the shell to the dorsolateral striatum. *Journal of Neuroscience*, *20*(6), 2369–2382.

Hampshire, A., & Owen, A. M. (2006). Fractionating attentional control using event-related fMRI. *Cerebral Cortex*, *16*(12), 1679–1689.

Mehta, M. A., Manes, F. F., Magnolfi, G., Sahakian, B. J., & Robbins, T. W. (2004). Impaired set-shifting and dissociable effects on tests of spatial working memory following the dopamine D2 receptor antagonist sulpiride in human volunteers. *Psychopharmacology (Berl)*, *176*(3–4), 331–342.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Reviews Neuroscience*, *24*, 167–202.

Mogg, K., Bradley, B. P., Hyare, H., & Lee, S. (1998). Selective attention to food-related stimuli in hunger: Are attentional biases specific to emotional and psychopathological states, or are they also found in normal drive states? *Behaviour Research and Therapy*, *36*(2), 227–237.

Morris, J. S., & Dolan, R. J. (2001). Involvement of human amygdala and orbitofrontal cortex in hunger-enhanced memory for food stimuli. *Journal of Neuroscience*, *21*(14), 5304–5310.

Ornstein, T. J., Iddon, J. L., Baldacchino, A. M., Sahakian, B. J., London, M., Everitt, B. J., et al. (2000). Profiles of cognitive dysfunction in chronic amphetamine and heroin abusers. *Neuropsychopharmacology*, *23*(2), 113–126.

Owen, A. M., Beksinska, M., James, M., Leigh, P. N., Summers, B. A., Marsden, C. D., et al. (1993). Visuospatial memory deficits at different stages of Parkinson's disease. *Neuropsychologia*, *31*(7), 627–644.

Owen, A. M., James, M., Leigh, P. N., Summers, B. A., Marsden, C. D., Quinn, N. P., et al. (1992). Fronto-striatal cognitive deficits at different stages of Parkinson's disease. *Brain*, *115*(6), 1727–1751.

Parkinson, J. A., Cardinal, R. N., & Everitt, B. J. (2000). Limbic cortico-ventral striatal systems underlying appetitive conditioning. In H. B. M. Uylings, C. G. Van Eden, J. P. C. De Bruin, M. G. P. Feenstra, & C. M. A. Pennartz (Eds.), *Progress in brain research* (Vol. 126, pp. 263–285). Amsterdam: Elsevier Science.

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Parkinson, J. A., Dalley, J. W., Cardinal, R. N., Bamford, A., Fehnert, B., Lachenal, G., et al. (2002). Nucleus accumbens dopamine depletion impairs both acquisition and performance of appetitive Pavlovian approach behaviour: Implications for mesoaccumbens dopamine function. *Behavioural Brain Research*, *137*(1–2), 149–163.

Roberts, A. C., Robbins, T. W., Everitt, B. J., & Muir, J. L. (1992). A specific form of cognitive rigidity following excitotoxic lesions of the basal forebrain in marmosets. *Neuroscience*, *47*(2), 251–264.

Rogers, R. D., Andrews, T. C., Grasby, P. M., Brooks, D. J., & Robbins, T. W. (2000). Contrasting cortical and subcortical activations produced by attentional-set shifting and reversal learning in humans. *Journal of Cognitive Neuroscience*, *12*(1), 142–162.

Rogers, R. D., Blackshaw, A. J., Middleton, H. C., Matthews, K., Hawtin, K., Crowley, C., et al. (1999). Tryptophan depletion impairs stimulus-reward learning while methylphenidate disrupts attentional control in healthy young adults: Implications for the monoaminergic basis of impulsive behaviour. *Psychopharmacology (Berl)*, *146*(4), 482–491.

Rogers, R. D., & Robbins, T. W. (2001). Investigating the neurocognitive deficits associated with chronic drug misuse. *Current Opinion in Neurobiology*, *11*(2), 250–257.

Volkow, N. D., Wang, G. J., Fowler, J. S., Logan, J., Jayne, M., Franceschi, D., et al. (2002). "Nonhedonic" food motivation in humans involves dopamine in the dorsal striatum and methylphenidate amplifies this effect. *Synapse*, *44*(3), 175–180.

Wager, T. D., Jonides, J., & Smith, E. E. (2006). Individual differences in multiple types of shifting attention. *Memory & Cognition*, *34*(8), 1730–1743.