



Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Neural correlates of affective influence on choice

Richard M. Piech^{a,*}, Jade Lewis^a, Caroline H. Parkinson^a, Adrian M. Owen^b, Angela C. Roberts^c, Paul E. Downing^a, John A. Parkinson^a^aSchool of Psychology, Bangor University, LL57 2AS, UK^bMRC Cognition and Brain Sciences Unit, Cambridge, UK^cDepartment of Physiology, Development and Neuroscience, University of Cambridge, UK

ARTICLE INFO

Article history:

Accepted 28 September 2009

Available online xxxx

Keywords:

Food choice
Decision making
Hunger
Motivation
fMRI
Affect

ABSTRACT

Making the right choice depends crucially on the accurate valuation of the available options in the light of current needs and goals of an individual. Thus, the valuation of identical options can vary considerably with motivational context. The present study investigated the neural structures underlying context dependent evaluation. We instructed participants to choose from food menu items based on different criteria: on their anticipated taste or on ease of preparation. The aim of the manipulation was to assess which neural sites were activated during choice guided by incentive value, and which during choice based on a value-irrelevant criterion. To assess the impact of increased motivation, affect-guided choice and cognition-guided choice was compared during the satiated and hungry states. During affective choice, we identified increased activity in structures representing primarily valuation and taste (medial prefrontal cortex, insula). During cognitive choice, structures showing increased activity included those implicated in suppression and conflict monitoring (lateral orbitofrontal cortex, anterior cingulate). Hunger influenced choice-related activity in the ventrolateral prefrontal cortex. Our results show that choice is associated with the use of distinct neural structures for the pursuit of different goals.

Published by Elsevier Inc.

1. Introduction

Our everyday lives consist of a stream of choices. By the time we arrive at work in the morning, we have already selected a shirt, a route, and coffee with or without cream. Many choices are made with some degree of automaticity, but others are preformed in a consciously controlled manner, as they require a flexible adaptation to the current task. The present study addresses such choices. Making appropriate choice decisions depends crucially on the accurate valuation of the available options in the light of attaining the current goals of an individual. These goals can be manifold: they can consist of achieving physiological homeostasis like relieving hunger feelings, or be more abstract, like beating a friend at chess. Notably, the valuation of – sometimes identical – choice options depends on the current needs of the individual (Ferguson & Bargh, 2004). So, for example, hunger might drive or even facilitate meal preparation, but interfere with completing a chess victory.

Dual-process models of decision making distinguish between two kinds of conscious choices: humans can arrive at decisions

by virtue of effortful, rule-based reasoning, or by intuitive, heuristic processes (Kahneman, 2003; Sloman, 1996). In agreement with such a model, Goel and Dolan (2003) dissociated rational, ‘cold’ choices from ‘hot’ ones, influenced by affective value. Their study included choice options that were logically equivalent but loaded to a different degree with affective value. They showed reciprocal responses in the ventral medial prefrontal cortex (ventral mPFC) and lateral PFC. Increased activity in the ventral mPFC was associated with ‘hot’ choices, which also decreased activity in the lateral PFC. The reverse response pattern was associated with ‘cold’ choices. Similarly, Winston and colleagues (Winston, Strange, O’Doherty, & Dolan, 2002) showed enhanced activity in the ventral mPFC and the somatosensory cortex when emotional information processing was the participants’ goal rather than when it happened incidentally.

The representation of affective value itself in the human brain has been studied utilizing brain imaging recordings of responses, in most cases, positive stimuli including primary reinforcers like food, smell and flavor (Anderson et al., 2003; Small & Prescott, 2005; Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001), but also pleasant pictures (Garavan, Pendergrass, Ross, Stein, & Risinger, 2001), and abstract stimuli associated with reward, like descriptions of food (Arana et al., 2003). These and other studies suggest a network of structures, including the amygdala, the basal

* Corresponding author. Present address: Department of Psychology, Vanderbilt University, PMB 407817, 2301 Vanderbilt Place, Nashville, TN 37240-7817, USA. Fax: +1 615 343 8449.

E-mail address: r.piech@vanderbilt.edu (R.M. Piech).

ganglia, the PFC, the insula and the anterior cingulate to represent different aspects of value.

An important question provoked by these findings is of how different aspects of value representation guide choice processes, and which neural structures are involved in their computation. Arana et al. (2003) found increased activation in the medial orbitofrontal cortex (mOFC) and the medial striatum in a condition which required choosing, in addition to evaluating food options. Paulus and Frank (2003) showed that a beverage preference judgment engaged the ventral mPFC, the anterior insula and sections of the parietal and cingulate cortices more strongly than a visual discrimination task. While these studies suggest structures which underlie evaluation and choice processes, critically they do not directly contrast choice behavior when salient options were affectively laden versus choices that were non-affective but otherwise equivalent in nature. The current study was intended to address this issue. In particular, it was designed to identify neural sites active during choice behavior that is guided by an affective process – the assignment of an incentive value to a stimulus, and during choice guided by a cognitive process – the employment of an effortful, rule-based computation.

For the present study, we chose to explicitly control the basis of choice by instructing participants to use a specific criterion – affective or non-affective – to guide their choice while selecting from restaurant meal options. The actual stimuli present were identical, i.e. this study attempted to extract out structures involved specifically in utilizing affective (or cognitive) information in an otherwise equivalent choice situation. Participants completed the following task while undergoing an fMRI recording. They were asked to imagine being in a restaurant and studying the menu to make a selection. During each experimental trial, they were presented three menu items. Their task was to read each item description, to imagine it, and to choose one of them. The critical manipulation was implemented through an instruction prior to each trial: in half the cases, participants were asked to choose which item they would like to *order and eat* if they were actually in a restaurant ('eat' condition). In the other half of the trials, participants were instructed to choose which item they consider the *easiest to cook* ('cook' condition). Thus, both conditions required a consideration of the properties of the dishes and a selection process. In the first condition, however, choices were guided by affective properties, in the second by cognitive-procedural properties of the stimuli.

The 'eat' condition in our study represents processes of affect-guided choice. The investigation of affective influences on choice, especially in the context of food selection, needs to consider the relationship between value and motivation. In particular, the affective value of an option may be susceptible to changes driven by an altered motivational state. So whilst, in both the 'eat' and 'cook' conditions, the choice required using appropriate motivational and cognitive systems to make the response, in the 'eat' condition the choice was based on the projected rewarding quality of the menu item value, whereas in the 'cook' condition the choice had to be based on cognitive knowledge of procedures required for the preparation of a dish. Several studies have shown that altering the motivational state of participants by changing their hunger level has an impact on decision making and neural responses associated with relevant stimuli (Hinton et al., 2004; Killgore & Yurgelun-Todd, 2006; Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Small et al., 2001). A further goal of our study was to investigate whether neural activity during choice guided by affective information was susceptible to manipulation of motivation. Therefore, we conducted the experiment in two otherwise identical sessions, one during which participants were sated, and one in which they were hungry. We hypothesized that the increased motivation to eat would have an impact on the processes involved in choosing

food based on its expected reward properties, but not based on the procedural properties of its preparation.

In summary, participants in the current study made selections from restaurant menu items presented on a screen, once while they were hungry and once while sated. They were instructed to make their selection based on either the desirability of the dishes or the complexity of their preparation. Thus, two experimental factors were manipulated, the motivational state of the participants and the affective value of the information to be processed. We predicted that motivational state should influence processes involved in the 'eat' food choice, but would not affect cooking complexity choices.

2. Method

2.1. Design

Eight volunteers (three female; group average age of 27.9, SD = 4.1) participated in three experimental sessions. These were the same participants as in a parallel study published elsewhere (Piech et al., 2009). They underwent fMRI recording during two one-hour sessions, one in the hungry, and one in the sated condition. The two recordings happened ca. 1 week apart, and the sequence of conditions was balanced for all participants. For the hungry condition, participants were instructed to not eat for 6 h prior to the experiment. In an initial session, participants completed an extended questionnaire indicating their food preferences. The information from it was then used to design individual menu choice options for the main experiment, which would include a variety of items, excluding items evoking negative responses like disgust. Each session consisted of three blocks of approximately 12 min length. Immediately after the recording, participants reported their hunger level on a visual analogue scale, which was scored between 0 (not hungry at all) and 100 (extremely hungry). They were debriefed after the second session and paid for their time. The study was approved by Research Ethics Committee of the University of Wales, Bangor.

2.2. Task

Participants were asked to imagine being in a restaurant for an evening meal. While in the scanner, they were presented with three dish descriptions from restaurant menus in each trial, with all three presented on one screen (on top, middle, and bottom of screen; no actual food was presented). The text was back-projected on a screen and viewed through a mirror. Participants were instructed to study the menu items to make a selection, using a response box held in their right hand. Their task depended on an instruction which appeared on the screen prior to each trial. For the 'eat' condition, participants' task was to read each item description, and to choose the one they would select in a restaurant. For the 'cook' condition, the selection was to be based on the complexity of preparation, i.e. participants were asked to choose the one which they thought would be the easiest to cook. The order of trials was randomized. Participants indicated their choice by pressing the top, middle or bottom key on a keypad. An example of three choice options would be: (1) "Tender roast lamb served with roast potatoes, cabbage, sweetcorn, and mint sauce." (2) "Succulent chunks of lamb in a thick creamy gravy with chestnut mushrooms, onions and leeks oven baked to perfection." (3) "Bite size chicken pieces marinated in sherry garlic, soy sauce and lemon juice. Served with assorted vegetables and rice." Each session consisted of 3 scans of 11 min, and 24 menu ratings per scan. Each menu selection appeared on the screen for 22 s after a trial instruction ('eat' or 'cook') of 1 to 2 s. The fixation interval between

presentations was randomly jittered between 1 and 3 s. Only the duration between item onset and response (i.e. not the entire 22 s) was modeled for the fMRI analysis.

2.3. fMRI data acquisition and analysis

A 1.5 T Philips MRI scanner was used to acquire 22 T2* weighted slices per volume (5 mm slices, resulting in 3.75 mm × 3.75 mm × 5 mm voxel size), with a repetition time of 2.2 s. The slices were tilted (anterior up) by 30° from the ACPC axial plane to reduce susceptibility artifacts. Thus the recorded volume included the entire brain volume excluding only ventral parts of the cerebellum. The first five volumes of each scan were discarded to avoid differences in T1-saturation. Preprocessing and statistical analysis were performed using BrainVoyager 2000 and BrainVoyager QX (Brain Innovation, The Netherlands). The functional images were slice-time acquisition corrected, subject motion corrected, spatially normalized to Talairach space (Talairach & Tournoux, 1988), and spatially smoothed with a 4 mm full width at half maximum Gaussian kernel. A correction for temporal autocorrelation and a temporal high pass filter of 0.01 Hz were applied. The two fMRI recordings took place approximately one week apart. Anatomical scans were acquired during both sessions to ensure accuracy of the intersession alignment of functional data.

The events for the fMRI signal were modeled as follows. For each event, duration always corresponded to the period from onset of the menu item to participants' individual trial choice response time (roughly 12 s, see results; upper limit 20 s). Since participants needed this relatively long period of time, and since they could be assumed to be making the actual choice towards the end of that period, we included an additional analysis method after initial inspection of the results. The method employed a stick-function analysis in which we only used the 10 ms prior to the response in each trial as the period of interest. The purpose of this analysis was to increase power to detect interactions between choice condition and motivational state. For the event-related fMRI analysis, eat and cook trials were modeled as separate events for both the sated and hungry sessions. This allowed the data to be analyzed as two factors with two conditions each: hunger state (hungry, sated) and task (eat, cook). Both sessions were entered in one analysis using dummy variables which remained empty in the non-relevant condition (e.g. the eat-hungry variable had no events for the sated session). The general linear model used for the fMRI data analysis thus included 11 regressors. These were two trial types (eat and cook), six motion regressors, and one artefact regressor. The eat and cook trials were entered twice, for the sated and the hungry session. The motion predictors included transitions along the three axes and rotations around them. The artefact regressor was entered at points where gross head movement was detected during visual inspection. Columns of the stimulus design matrix were convolved with a canonical hemodynamic response function. In order to identify activity peaks corresponding to the processes of interest, an unconstrained whole-brain random-effects analysis was conducted. Areas of functional activity were defined as clusters of 10 or more contiguous voxels which exceeded an uncorrected p -value of .0005. This is an arbitrary, while relatively stringent criterion. In the post hoc, stick-function analysis, we used a threshold of .005 to explore the activations representing task by state interactions. Our statistical analysis package allowed one method of accounting for multiple comparisons, the Bonferroni correction, which has been frequently described as overly conservative (Friston, Frith, Liddle, & Frackowiak, 1991). None of the whole-brain calculated activations reported here survive such a correction.

The number of participants is small due to the considerable complexity of the design. While many fMRI studies use larger

sample sizes, random-effects analyses with as few as six subjects are permitted (Holmes & Friston, 1998). The given sample size may produce only low statistical power and render null-effects unreliable. We therefore focus the interpretation of our results on positive effects.

3. Results

3.1. Behavioral analysis

Confirming the experimental manipulation, participants indicated higher levels of hunger after the scan in the hungry condition than after the scan in the sated condition (Hungry: 81, SE = 3.1; Sated: 22, SE = 3.0; $t(5) = 9.63$, $p < .0005$). The menu selection was paced by the participants with the average response times (and standard errors) being 12.7 s (1.2), 12.4 s (1.3), 12.1 s (1.4), and 12.0 s (1.5) for the 'hungry & eat', 'hungry & cook', 'sated & eat', and 'sated & cook' conditions, respectively. A repeated measures ANOVA indicated no response time differences between the conditions (F -values < 1.5).

3.2. Event-related fMRI analysis

3.2.1. Affect-guided and cognition-guided choice behavior

We expected that contrasting the data from the "cook" task from the data from the "eat" task would emphasize the impact of appetitive anticipatory processes on choice, while the opposite subtraction would emphasize utilization of cognitive information.

To this end, we conducted a whole brain contrast comparing activity elicited by the menu stimuli under the two task conditions, eat and cook, for both recording sessions. Increased activity was found in the "eat" task in the medial prefrontal cortex (mPFC, BA 10, $x = -6$, $y = 47$, $z = 22$, $t(7) = 7.60$, Fig. 1A), in the central part of the insula ($x = -36$, $y = 8$, $z = 10$, $t(7) = 6.33$), Fig. 1B), and in an area of the anterior temporal lobe, in the middle temporal sulcus (BA 21, $x = -57$, $y = -7$, $z = -8$, $t(7) = 6.69$, Fig. 1C). To confirm that the specified clusters responded more strongly to the conditions of interest, we computed averaged time courses of the BOLD signal for these sites (Fig. 1A–C).

The opposite contrast revealed more activity in the lateral OFC (BA 47, $x = -42$, $y = 32$, $z = -9$, $t(7) = 9.13$, Fig. 2A), in the anterior cingulate cortex (ACC, BA 24, $x = 0$, $y = 26$, $z = 7$, $t(7) = 6.30$, Fig. 2B), and in an area of the posterior temporal lobe (Middle temporal lobe, BA 20, $x = -63$, $y = -34$, $z = -11$, $t(7) = 8.48$, Fig. 2C). The averaged time courses for those clusters are shown in Fig. 2A–C.

To investigate the impact of motivational state on task related activity, we conducted an interaction analysis, with a contrast which would reveal areas activated more strongly for the eat condition, but only in the hungry state. That was achieved through a contrast which assigned positive weights to the eat condition and negative weights to the cook condition for the hungry session, as well as the reverse weights for the sated session. A whole brain analysis with these contrasts followed by inspection of the activation patterns of potentially involved areas showed that no such area could be identified, even at a liberal threshold of $p < .01$, with our original analysis. Our whole-brain exploratory stick-function analysis yielded a single significant activation, in the ventrolateral PFC, at a statistical threshold of $p < .005$ with a cluster size of more than 10 contiguous voxels (BA 47, $x = 44$, $y = 44$, $z = -2$, $t(7) = 5.1$, Fig. 3).

Overall, we found that affect-guided choice behavior activates a different set of areas compared to equivalent choice behavior when it is solely based on procedural information not related to value. An area of the ventrolateral PFC showed activation consistent with an interaction function between task and hunger state.

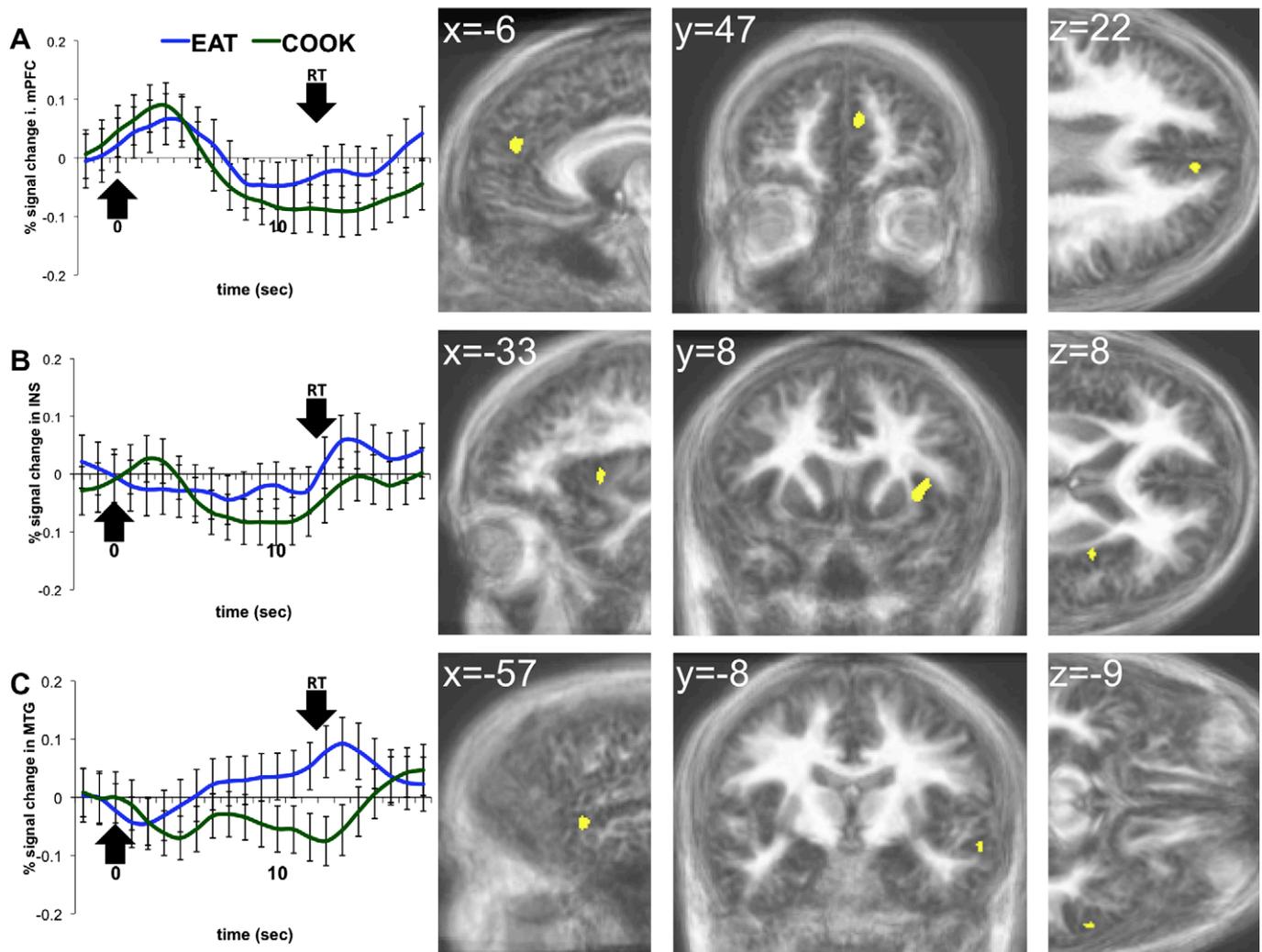


Fig. 1. Sites activated by affect-guided choice. Averaged time courses of the response to conditions 'eat' and 'cook' (left side of panels, arrows indicate stimulus onset, bars show the standard error), and respective activated clusters. (A) Medial prefrontal cortex, (B) the insula and (C) middle temporal gyrus. Activation maps are shown overlaid over averaged anatomical scans for all subjects. Activations were defined as clusters of 10 or more contiguous voxels which exceeded an uncorrected p -value of .0005. The above figure uses a more lenient threshold of $p < .005$ for demonstration purposes. The shown cluster extent threshold is 10 voxels. Averaged time courses illustrate the activity of the selected clusters, they are not an independent analysis. The arrows at time point 0 indicate the stimulus onset, arrows marked 'RT' indicate the mean response time.

4. Discussion

The affective choice condition in our study activated the mPFC, the insula, and an anterior site in the lateral temporal lobe (middle temporal gyrus, MTG), while the cognitive choice condition activated the lateral OFC, the anterior cingulate, and a site in the posterior part of the lateral temporal lobe (middle temporal sulcus, MTS). We also designed our experiment to be conducted in two sessions, while the participants were either sated or hungry in order to allow us to identify regions that show an interaction response pattern. We showed such an activation pattern in an area of the ventrolateral prefrontal cortex.

4.1. Affect-guided choice task

The function of the medial prefrontal cortex (mPFC) is the subject of much debate (Christoff & Gabrieli, 2000; Gilbert et al., 2006; Ramnani & Owen, 2004). Amodio and Frith (2006) describe the section of mPFC activated in our study as anterior rostral medial frontal cortex and suggest it plays a role in three categories of processes, involving self-knowledge, perception of other persons

and mentalizing. The last of these is also referred to as theory of mind (ToM) – thinking about what others think (Mitchell, Heather-ton, & Macrae, 2002; Völlm et al., 2006). Likewise, Gilbert et al. (2006) conducted a meta-analysis of over a hundred functional imaging studies which activated the mPFC (specifically BA 10) and concluded that this site is often associated with tasks that involve mentalizing and attending to one's own emotions, as opposed to more lateral and more rostral sites, involving memory processes and multi-tasking, respectively.

Montague, King-Casas, and Cohen (2006) review of literature on reward and valuation considers the mPFC (together with the ventral striatum and the OFC) a component of the ventral valuation network, and suggests that mPFC response often reflects the value of rewards, including a prospective valuation of predicted reward. In the current study, mPFC activation occurred during affectively guided choice, when representation of the anticipated reward value is necessary to make the correct decision. This is consistent with a role of that area in predictive valuation of stimuli (Montague et al., 2006). Within decision making literature, evaluating rewards is often associated with ventral sites of the mPFC, sometimes referred to as medial orbitofrontal cortex (Knutson,

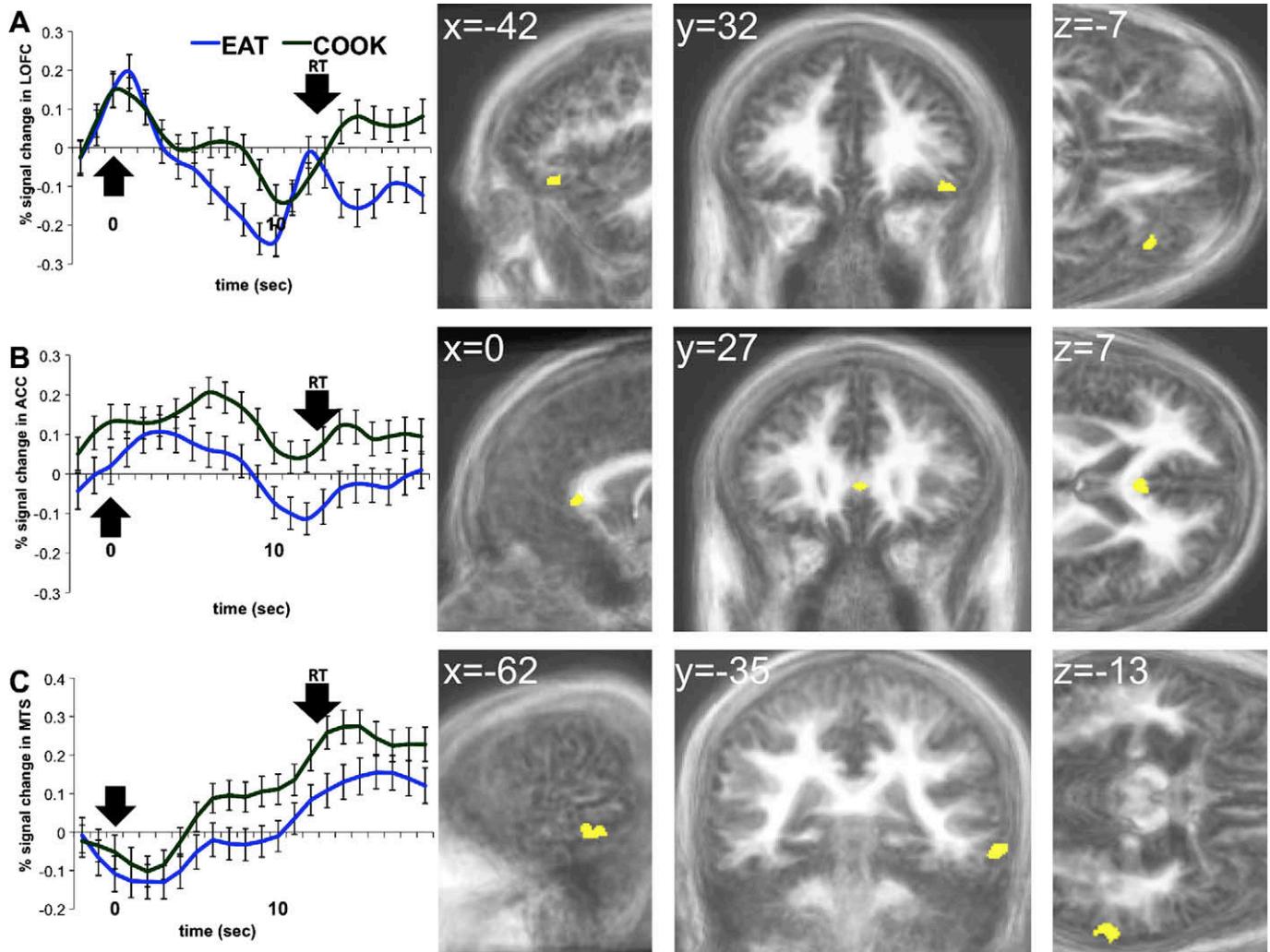


Fig. 2. Sites activated by cognition-guided choice. Averaged time courses of the response to conditions 'cook' and 'eat' (left side of panels, arrows indicate stimulus onset, bars show the standard error), and respective activated clusters. (A) Lateral orbitofrontal cortex, (B) anterior cingulate cortex and (C) middle temporal sulcus. Activation maps are shown overlaid over averaged anatomical scans for all subjects. Activations were defined as clusters of 10 or more contiguous voxels which exceeded an uncorrected p -value of .0005. The above figure uses a more lenient at a threshold of $p < .005$ for demonstration purposes. The shown cluster extent threshold is 10 voxels. Averaged time courses illustrate the activity of the selected clusters, they are not an independent analysis. The arrows at time point 0 indicate the stimulus onset, arrows marked 'RT' indicate the mean response time.

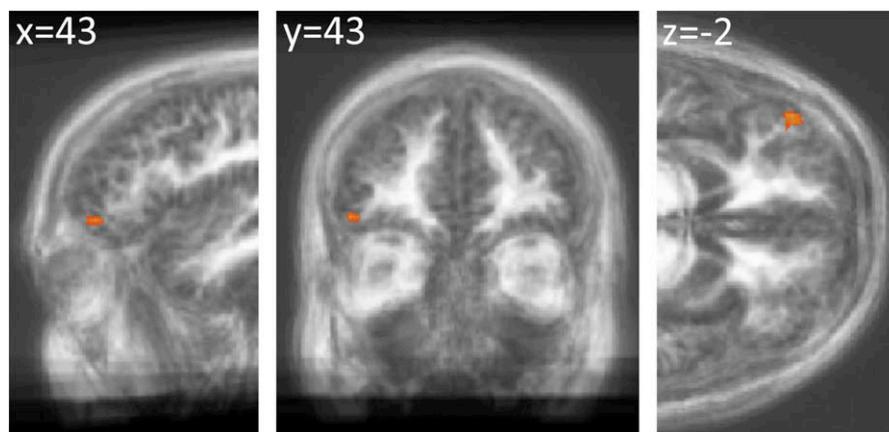


Fig. 3. Site showing an interaction between the choice task and hunger state. The activated cluster is in the ventrolateral PFC, likely within BA 47, the maximum peak at $x = 44, y = 44, z = -2$. Activation maps are shown overlaid over averaged anatomical scans for all subjects. Activation was defined as a cluster of 10 or more contiguous voxels which exceeded an uncorrected p -value of .005. The above figure uses a more lenient threshold of $p < .019$ for demonstration purposes.

Fong, Adams, Varner, & Hommer, 2001; Plassmann, O'Doherty, Shiv, & Rangel, 2008). Such activations are typically localized when stimuli of great value are contrasted with ones of lesser value, or as correlations with stimulus ratings. The mPFC activation reported here is localized at a more dorsal site (Fig. 1A). We believe that is because our contrast does not reflect sole value representation, as in each trial three stimuli of different values are present. Rather, our tasks portrays an affective evaluation process, possibly based on attending to one's own emotions and motivational needs (Christoff & Gabrieli, 2000; Gilbert et al., 2006; Steele & Lawrie, 2004). Another site which is activated in our study during affectively guided choice is the anterior temporal lobe. Activations of this site have also previously been implicated in evaluating events related to the self or others (Mitchell et al., 2002; Völlm et al., 2006), and may reflect judgments about the personal value of a prospective meal, including attempts to infer the consequences and hence mental and physiological state of the self following a particular meal.

The insular cortex subserves a variety of functions related to interoception (Craig, 2002; Critchley, Wiens, Rotshtein, Oehman, & Dolan, 2004) and the perception of taste and its reward qualities (de Araujo & Rolls, 2004). Chaudhry, Parkinson, Hinton, Owen, and Roberts (2009) have recently shown that affective evaluation of more abstract stimuli than ours (holidays), activates a similar area of the insula (albeit in the right hemisphere). Most notably, it has been shown to represent interactions of reward value with motivational states (Hinton et al., 2004; Small et al., 2001). The activation of the insula found during affect-guided choice in our study is likely to represent expected sensory gustatory qualities of the presented items, upon which the decision regarding which item would be most preferred to eat must be based.

4.2. Cognition-guided choice task

In the current task, the cognitive contrast yielded activity in the lateral OFC. The OFC is broadly thought to represent reward value (Rolls, 2000), as it has been shown to respond to a number of positive stimuli, among them tastes and odors. Besides that, the OFC has also been shown to represent negative stimuli, and reward value change (Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Small et al., 2001). This combination of observations has led to claims that the OFC represents both primary reinforcer value and processes associated with incorporating changes in value brought about by fluctuating motivation, and hence in the control and correction of behavior driven by reward (Rolls, 2000).

The area in the lateral OFC activated in the current study maps well onto previous findings: Small et al. (2001) observed in their study that as the value of a food (chocolate) decreased with consumption, activity in the lateral OFC increased, suggesting that it represented aversive value. O'Doherty and colleagues (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001) came to a similar conclusion, as their value reversal learning task produced lateral OFC responses to punishing stimuli. Using a logical reasoning task, Goel and Dolan (2003) dissociated lateral from medial PFC on the basis of emotional salience: purely logical judgments engaged lateral PFC, whilst those involving emotional content activated medial PFC. Elliott, Dolan, and Frith (2000) reviewed work on OFC function and concluded that the results are consistent with the suppression of a previously rewarded response in the lateral OFC. In the current study, lateral OFC was activated during cognitively guided choice, when it is appropriate to ignore or suppress the reward value of the food items and the choice decision needs to be based on a different criterion. A parsimonious explanation of the current findings therefore is that lateral OFC supports cognitively driven judgments and may operate antagonistically with affect-based medial circuitry.

The ACC has been implicated in an array of functions, including processing of sensory, motor, emotional and cognitive information. A common denominator in ACC function appears to be the monitoring of conflict (Botvinick, Cohen, & Carter, 2004). In an attempt to specify the function of the ACC and its subdivisions, Bush and colleagues (Bush, Luu, & Posner, 2000) reviewed findings from neuroimaging, lesion and physiological studies. They suggested a separation of the ACC in dorsal and ventral areas, corresponding to Brodmann areas 24 and 32, with the dorsal division frequently active in cognitive tasks, and the (rostral-) ventral areas involved in affective tasks. The activation peak we identified in the ACC for cognition-guided choice falls into the rostral-ventral division of BA 32. In agreement with the cited work, it might represent an affective conflict monitoring process. This is a plausible explanation if one assumes that the affective representation of the choice options potentially occurs automatically, and that it is a process which during the cognitively guided choice might create a conflict. This interpretation of the ACC activity would converge with the activation in the lateral OFC found in the same condition.

In the light of the dual-process model of decision making (Kahneman, 2003; Slovic, 1996), our 'eat' condition could be referred to as an intuitive choice, based on one's liking of a dish. The 'cook' condition however, required more effortful reasoning to allow choosing between the complexity of different cooking procedures, and thus constitutes an effortful, rule-based choice. Within the PFC, we found a medial activation for the intuitive choice, and a lateral activation for the rule-based choice. This is consistent with the results of other studies, which also found the medial PFC to be activated by processes related to heuristic processes incorporating emotional evaluation (Goel & Dolan, 2003; Winston, Strange, O'Doherty, & Dolan, 2002) and it shows that employment of the rule-based and intuitive systems can be evoked by direct instructions.

4.3. Choice task and hunger state interaction

Our stick-function analysis revealed a site in the ventrolateral PFC, likely within BA 47, which showed an interaction between the task and state factors. Inspection of the beta-values suggested that activation was increased in the eat condition when participants were hungry, while the reverse pattern appeared for the sated state. The ventrolateral PFC has been previously reported to be active during affective evaluation of stimuli (Cunningham, Johnson, Gatenby, Gore, & Banaji, 2003; Cunningham, Raye, & Johnson, 2004; Jacobsen, Schubotz, Hoefel, & Cramon, 2006; Maddock, Garrett, & Buonocore, 2003), but to our knowledge no influences of motivational state on these have been reported to this date. As such, we report a novel and interesting neural locus reflecting the relationship between motivation and evaluative choice, as predicted by theories of goal-directed action Ferguson (de Wit & Dickinson, 2009; Ferguson & Bargh, 2004).

5. Conclusion

In the current study, we instructed participants to choose food menu items based on their anticipated taste or ease of preparation, aiming to elicit affect-guided and cognition-guided choice. During affective choice, structures representing primarily taste and valuation (mPFC, the insula) as well as an area of anterior temporal lobe were active. During cognitive choice, the structures used involved ones implicated in suppression and conflict monitoring. These results shed important insight into neural mechanisms of prospective choice behavior and support dual-process models of decision-making based on the affective content of the material. The relative activity of neural circuitry engaged in processing text-based food

descriptions differed depending on the nature of the choice to be made and suggests that decisions requiring input from motivational systems recruits medial prefrontal structures whilst those requiring the suppression of this information in favor of rule-based processing activates lateral prefrontal structures and the ACC. Finally, we indicate a role of the ventrolateral prefrontal cortex in the motivational modulation of choice processes.

Acknowledgments

We thank Tony Bedson and radiography staff at the Magnetic Resonance Unit at Ysbyty Gwynedd in Bangor, an anonymous reviewer for analysis suggestions, and Maureen McHugo for assistance with the analysis.

References

- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, 7(4), 268–277.
- Anderson, A. K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D. G., Glover, G., et al. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature Neuroscience*, 6(2), 196–202.
- Arana, F. S., Parkinson, J. A., Hinton, E., Holland, A. J., Owen, A. M., & Roberts, A. C. (2003). Dissociable contributions of the human amygdala and orbitofrontal cortex to incentive motivation and goal selection. *Journal of Neuroscience*, 23(29), 9632.
- Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, 8(12), 539–546.
- Bush, G., Luu, P., & Posner, M. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, 4, 215–222.
- Chaudhry, A., Parkinson, J., Hinton, E., Owen, A., & Roberts, A. (2009). Preference judgements involve a network of structures within frontal, cingulate and insula cortices. *European Journal of Neuroscience*, 29(5), 1047.
- Christoff, K., & Gabrieli, J. D. E. (2000). The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology*, 28(2), 168–186.
- Craig, A. D. (2002). How do you feel? interoception: The sense of the physiological condition of the body. *Nature Reviews Neuroscience*, 3, 655–666.
- Critchley, H. D., Wiens, S., Rotshtein, P., Oehman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, 7(2), 189–195.
- Cunningham, W., Johnson, M., Gatenby, J., Gore, J., & Banaji, M. (2003). Neural components of social evaluation. *Journal of Personality and Social Psychology*, 85(4), 639–649.
- Cunningham, W., Raye, C. L., & Johnson, M. K. (2004). Implicit and explicit evaluation: fMRI correlates of valence, emotional intensity, and control in the processing of attitudes. *Journal of Cognitive Neuroscience*, 16(10), 1717–1729.
- de Araujo, I. E., & Rolls, E. T. (2004). Representation in the human brain of food texture and oral fat. *Journal of Neuroscience*, 24(12), 3086.
- de Wit, S., & Dickinson, A. (2009). Associative theories of goal-directed behaviour: A case for animal-human translational models. *Psychological Research*, 73(4), 463–476.
- Elliott, R., Dolan, R. J., & Frith, C. D. (2000). Dissociable functions in the medial and lateral orbitofrontal cortex: Evidence from human neuroimaging studies. *Cerebral Cortex*, 10(3), 308–317.
- Ferguson, M., & Bargh, J. (2004). Liking is for doing: The effects of goal pursuit on automatic evaluation. *Journal of Personality and Social Psychology*, 87, 557–572.
- Friston, K., Frith, C., Liddle, P., & Frackowiak, R. (1991). Comparing functional (PET) images: The assessment of significant change. 1. *Journal of Cerebral Blood Flow and Metabolism*, 11, 10.
- Garavan, H., Pendergrass, J. C., Ross, T. J., Stein, E. A., & Risinger, R. C. (2001). Amygdala response to both positively and negatively valenced stimuli. *NeuroReport*, 12(12), 2779–2783.
- Gilbert, S. J., Spengler, S., Simons, J. S., Steele, J. D., Lawrie, S. M., Frith, C. D., et al. (2006). Functional specialization within rostral prefrontal cortex (Area 10): A meta-analysis. *Journal of Cognitive Neuroscience*, 18(6), 932–948.
- Goel, V., & Dolan, R. J. (2003). Reciprocal neural response within lateral and ventral medial prefrontal cortex during hot and cold reasoning. *NeuroImage*, 20(4), 2314–2321.
- Hinton, E. C., Parkinson, J. A., Holland, A. J., Arana, F. S., Roberts, A. C., & Owen, A. M. (2004). Neural contributions to the motivational control of appetite in humans. *European Journal of Neuroscience*, 20(5), 1411–1418.
- Holmes, A., & Friston, K. (1998). Generalizability, random effects, and population inference. *NeuroImage*, 7, 1.
- Jacobsen, T., Schubotz, R., Hoefel, L., & Cramon, D. (2006). Brain correlates of aesthetic judgment of beauty. *NeuroImage*, 29(1), 276–285.
- Kahneman, D. (2003). A perspective on judgment and choice: Mapping bounded rationality. *American Psychologist*, 58(9), 697–720.
- Killgore, W. D., & Yurgelun-Todd, D. A. (2006). Affect modulates appetite-related brain activity to images of food. *International Journal of Eating Disorders*, 39(5), 357–363.
- Knutson, B., Fong, G., Adams, C., Varner, J., & Hommer, D. (2001). Dissociation of reward anticipation and outcome with event-related fMRI. *NeuroReport*, 12, 5.
- Kringelbach, M. L., O'Doherty, J., Rolls, E. T., & Andrews, C. (2003). Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cerebral Cortex*, 13(10), 1064–1071.
- Maddock, R., Garrett, A., & Buonocore, M. (2003). Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. *Human Brain Mapping*, 18(1), 30–41.
- Mitchell, J. P., Heatherton, T. F., & Macrae, C. N. (2002). Distinct neural systems subserve person and object knowledge. *Proceedings of the National Academy of Sciences*, 99(23), 15238.
- Montague, P. R., King-Casas, B., & Cohen, J. D. (2006). Imaging valuation models in human choice. *Annual Reviews Neuroscience*, 29, 417–448.
- O'Doherty, J., Kringelbach, M. L., Rolls, E. T., Hornak, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature Neuroscience*, 4, 95–102.
- Paulus, M. P., & Frank, L. R. (2003). Ventromedial prefrontal cortex activation is critical for preference judgments. *NeuroReport*, 14(10), 1311–1315.
- Piech, R., Lewis, J., Parkinson, C., Owen, A., Roberts, A., Downing, P., et al. (2009). Neural correlates of appetite and hunger-related evaluative judgments. *PLoS ONE*, 4(8), e6581. doi:10.1371/journal.pone.0006581.
- Plassmann, H., O'Doherty, J., Shiv, B., & Rangel, A. (2008). Marketing actions can modulate neural representations of experienced pleasantness. *Proceedings of the National Academy of Sciences*, 105(3), 5.
- Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. *Nature Reviews Neuroscience*, 5(3), 184–194.
- Rolls, E. T. (2000). The orbitofrontal cortex and reward. *Cerebral Cortex*, 10(3), 284–294.
- Slooman, S. A. (1996). The empirical case for two systems of reasoning. *Psychological Bulletin*, 119(1), 3–22.
- Small, D. M., & Prescott, J. (2005). Odor/taste integration and the perception of flavor. *Experimental Brain Research*, 166(3), 345–357.
- Small, D. M., Zatorre, R. J., Dagher, A., Evans, A. C., & Jones-Gotman, M. (2001). Changes in brain activity related to eating chocolate: From pleasure to aversion. *Brain*, 124(9), 1720.
- Steele, J. D., & Lawrie, S. M. (2004). Segregation of cognitive and emotional function in the prefrontal cortex: A stereotactic meta-analysis. *NeuroImage*, 21(3), 868–875.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic axis of the human brain*. New York: Thieme.
- Völlm, B. A., Taylor, A. N. W., Richardson, P., Corcoran, R., Stirling, J., McKie, S., et al. (2006). Neuronal correlates of theory of mind and empathy: A functional magnetic resonance imaging study in a nonverbal task. *NeuroImage*, 29(1), 90–98.
- Winston, J. S., Strange, B. A., O'Doherty, J., & Dolan, R. J. (2002). Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nature Neuroscience*, 5(3), 277–283.