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Human striatal activation during adjustment of the response criterion in visual word recognition

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ABSTRACT

Results of recent computational modelling studies suggest that a general function of the striatum in human cognition is related to shifting decision criteria in selection processes. We used functional magnetic resonance imaging (fMRI) in 21 healthy subjects to examine the hemodynamic responses when subjects shift their response criterion on a trial-by-trial basis in the lexical decision paradigm. Trial-by-trial criterion setting is obtained when subjects respond faster in trials following a word trial than in trials following nonword trials — irrespective of the lexicality of the current trial. Since selection demands are equally high in the current trials, we expected to observe neural activations that are related to response criterion shifting. The behavioural data show sequential effects with faster responses in trials following word trials compared to trials following nonword trials, suggesting that subjects shifted their response criterion on a trial-by-trial basis. The neural responses revealed a signal increase in the striatum only in trials following word trials. This striatal activation is therefore likely to be related to response criterion setting. It demonstrates a role of the striatum in shifting decision criteria in visual word recognition, which cannot be attributed to pure error-related processing or the selection of a preferred response.

Introduction

The role of the basal ganglia in higher cognitive processing remains a matter of debate. Basal ganglia are known to support error correction (Lawrence, 2000) and prediction error processing (O'Doherty et al., 2004), response preparation (Monchi et al., 2001), and, more generally, basal ganglia functioning are associated with the planning of actions (Glover, 2004) and action selection (Grillner et al., 2005; Jüptner and Weiller, 1998; Redgrave et al., 1999). Recent neuroimaging research has revealed basal ganglia involvement in higher cognitive tasks such as decision making (Grinband et al., 2006), verbal processing (Friederici and Kotz, 2003; Friederici, 2006; Schirmer, 2004) and semantics (such as word generation; Crosson et al., 2003; 2007). Taken together, these data on basal ganglia involvement in different cognitive functions point to a substantial role of the basal ganglia in higher cognitive processes (Crosson et al., 2007).

More recently, modelling studies (Bogacz, 2007; Bogacz and Gurney, 2007; Lo and Wang, 2006) and imaging studies (e.g. Forstmann et al., 2008) have presented evidence that one function of the basal ganglia, and in particular the striatum, is in tuning decision criteria. Response criterion setting on a trial-by-trial basis can be used in decision making to optimize behaviour, for example to control the trade-off between speed and accuracy in simple reaction time tasks and perceptual tasks (Gold and Shadlen, 2007; Smith and Ratcliff, 2004). Models of sequential sampling of information assume that noisy information is integrated over time until a criterion is reached that favours one response over another and stops the decision process (Lo and Wang, 2006; Smith and Ratcliff, 2004). These criteria can be set on a trial-by-trial basis to account for the variability in the stimulus quality. One hypothesis to explain how the basal ganglia affect selection processes refers to the setting of the response criterion in favour of a particular action, e.g. a manual response, depending on the outcome of a fronto-striatal processing loop (Crosson et al., 2003). Thus, (pre-)frontal brain regions might process the contextual cues of a decision task — and, depending on the occurrence of a cue, top down processing elicits strategic shifts or criterion settings that are expected to be processed in the basal ganglia (e.g. Braver and Barch, 2002; Gold and Shadlen, 2007). For example, using a perceptual decision task, Forstmann et al. (2008) could show that brain activation in the striatum covaries with individual adjustments in the response criterion.

Here, we want to add neuroimaging evidence to this debate by demonstrating, that the striatum is particularly activated when subjects adjust their response criterion on a trial-by-trial basis in a

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visual word recognition task: The lexical decision task (LDT) in which subjects have to decide upon the lexicality of a visually presented letter string is probably the most influential paradigm in the visual word recognition literature (Grainger and Jacobs, 1996). Despite the fact that the LDT can be used to examine the factors that contribute to single word comprehension, it is well known that the LDT is also prone to strategic effects. It has been shown that in a series of lexical decision trials, subjects tend to adjust their response criterion on a trial-by-trial basis depending on the lexical status of the last trial (Lima and Huntsman, 1997; Perea and Carreiras, 2003, also see Taylor and Lupker, 2001, for similar effects in visual word recognition using a naming task).

When subjects perform a LDT and try to follow the instruction to respond as fast as possible, they adjust their response criterion in order to optimize performance in each trial, e.g. to reduce response times while maintaining an acceptable level of accuracy (Perea and Carreiras, 2003; Perea and Estévez, 2006). Thus, when the response criterion has been successfully employed on the last trial, and the subject believes that his/her response was accurate, it can be lowered on the current trial (Perea et al., 2004). In particular, it is proposed that subjects monitor the passage of time during the processing of the task to flexibly adapt the point in time when a response is initiated (Lupker et al., 1997). The observed sequential dependencies suggest that such a time criterion can be adapted on a trial-by-trial basis when subjects follow the instruction to respond as fast as possible (Perea and Carreiras, 2003). Following a series of naming experiments using different types of word and nonword stimuli, Taylor and Lupker (2001) discussed the time criterion to be particularly lowered following easy to process trials (see also Mozer et al., 2007). Therefore, trials following a word trial lead to a faster response than trials following a nonword trial — irrespective of the lexical status of the current trial, and these effects do not result from an opposition of switch and non-switch trials. Sequential dependencies in the LDT can, therefore, not be explained by a motor-related congruency effect such as the Gratton-effect in the Erikson flanker task (Botvinick et al., 1999; Gratton et al., 1992).

In the present study we investigated the neural substrates underlying these sequential effects in the LDT. We expected that activation in the striatum is systematically increased in trials that lead to an adjustment of the response criterion, i.e. we expected to find faster responses and stronger striatum activation in trials that follow word trials compared with trials that follow nonword trials.

Materials and methods

Participants

Twenty-one right-handed healthy subjects from Bremen University (age ranging from 20 to 30 years, mean = 25.43 years, 19 females) participated in the study. A written informed consent was received from each subject, and the study was in accordance with the guidelines of the local ethics committee. Subjects were native German speakers, had normal or corrected-to-normal vision, and reported no history of drug abuse, neurological or psychiatric diseases or present psychotropic medication.

Experimental paradigm

In the fMRI scanner, the experiment was divided in two parts: a short training session comprising 10 trials to familiarize the subjects with the task, and the main experiment comprising 168 word and 168 nonword trials. Words and nonwords were matched on their number of letters, number of orthographic neighbours and mean bigram frequency known to affect lexical decision performance (Hofmann et al., 2007). All stimuli were presented in a pseudo-randomised order (counterbalanced for equal numbers of word/word, word/nonword, nonword/word, and nonword/nonword stimulus sequences) so that no more than three words or nonwords appeared consecutively.

A trial lasted on average 3000 ms consisting of the presentation of a fixation cross ('+') for 500 ms, the stimulus presentation in the center of the screen until button press (or a maximum of 2000 ms) and the re-appearance of the fixation cross for 300 ms plus a random, non-uniformly jittered intertrial interval (mean 200 ms, range 0 to 500 ms,). During stimulus presentation (Presentation™, Neurobehavioral Systems Inc.), subjects were instructed to judge as fast as possible whether the presented letter string is a word or a nonword by pressing one of two response buttons. No mention was made on sequential dependencies. Response times and errors were recorded, and afterwards analysed using the statistical software package SPSS™. Response times faster than 300 ms or slower than 2000 ms were defined as outliers and removed from all subsequent analyses. In addition, error trials and the trials following an error trial were removed from the response times and functional analyses to prevent the data from being related to error processing. The significance threshold was set a-priori at $p = 0.05$.

Data acquisition/analysis

fMRI data were acquired on a 3-T SIEMENS Magnetom™ Allegra system (Erlangen, Germany) scanner. A gradient-recalled echo-planar-imaging sequence optimized for blood oxygenation level-dependent contrasts was used with the following parameters: 38 slices; repetition time, 2000 ms; echo time, 29 ms; field of view, 192 mm; flipped angle, 80°; in-plane resolution, 3×3 mm^2; slice thickness, 3 mm; no interslice gap; interleaved acquisition order. During fMRI acquisition, stimuli were presented using an LCD projector (JVC G15E, XGA-resolution) rear-projecting the stimuli onto a screen located near the subjects head, visible via a mirror mounted on the head coil of the fMRI scanner, at a distance approximately 30 cm from the projection screen.

The functional data were preprocessed using SPM2 (http://www.fil.ion.ucl.ac.uk/spm; Wellcome Department of Cognitive Neurology, London, UK), running on Matlab 6.5 (Math Works, Natick, MA). The first 4 volumes of each section were discarded from the analysis to include only EPI images with an optimized signal. Preprocessing comprised the following steps: (1) slice time correction, (2) spatial realignment using a 2nd degree B-Spline, (3) normalisation to Montreal Neurological Institute (MNI) stereotactic space ($3 \times 3 \times 3$ mm), and (4) smoothing with a filter of 8 mm (full-width half-maximum) to account for anatomical differences between subjects and to allow for valid statistical inference at the group level.

Stimulus onsets of the experimental conditions were modelled with delta functions for words that followed a word trial (w–w), words that followed a nonword trial (nw–w), nonwords that followed a word trial (w–nw), nonwords that followed a nonword trial (nw–nw), and a rest category including all outliers, error trials and the trials following an error trial. These are convolved with the canonical hemodynamic response function specified in SPM2 to form the regressors. At the single-subject level a general linear model was computed comprising the four experimental regressors, the rest category, and six rotational and translational parameters obtained during image realignment as separate nuisance regressors of no interest. The serial autocorrelation of the blood oxygen level-dependent (BOLD) time series was modelled using a first-order autoregressive model, and the high-pass filter was set to 1/120 Hz. Linear contrasts were computed to analyse the main effects of lexicality of the current trial [(w–w), (nw–w), (w–nw), (nw–nw); contrast: (1 1 −1 −1)], lexicality of the last trial [(1 −1 1 −1)], and their two-way interaction [(1 −1 −1 1)]. T-tests were computed at the second-level group analysis, reporting significant effects at $p < 0.001$ (uncorrected) that exceed an extent threshold of $k \geq 10$ contiguous voxels. To further examine the sequential dependencies,

effects of the last trial were computed separately for current word and nonword trials at a $p<0.001$ (uncorrected, $k\geq 10$).

Results

Behavioural results

Response times and errors were subjected to a two-factorial repeated measures ANOVA. 5.5% of all observations were removed following the outlier procedure. Words and nonwords differed significantly in their response times [$F(1,20)=72.207$, $p<0.001$, $\eta^2=0.783$] due to faster responses for words. Within word trials (Fig. 1a), trials preceded by a word (w–w: 696 ms) were processed significantly faster compared to trials preceded by a nonword (nw–w: 723 ms; $T(20)=-7.972$, $p<0.001$). Similarly, within nonword trials (Fig. 1b), responses to trials preceded by a word (w–nw: 831 ms) were significantly faster compared to trials preceded by a nonword (nw–nw: 855 ms; $T(20)=-7.913$, $p<0.001$). In addition, stimulus lexicality did not affect error data [$F(1,20)=1.664$, $p=0.212$, $\eta^2=0.077$]. Although trials that were preceded by a word elicited slightly more errors, this sequential effect did not reach significance, neither within words trials (w–w: 0.025; nw–w: 0.020; $T(20)=-1.261$, $p=0.222$) nor within nonword trials (w–nw: 0.034; nw–nw: 0.031; $T(20)=-1.784$, $p=0.090$) possibly due to the overall low error rates. To further elaborate this result, simple regressions were computed to examine error rates as a function of response time. In word and nonword trials preceded by a word trial, we found a higher negative correlation between error rates and response times compared to trials preceded by a nonword trial. This data might suggests the occurrence of a speed-accuracy trade-off following word trials (see Fig. 1c, supplemental online material) though none of these correlations reached statistical significance (w–w: $r=-0.163$; $p=0.481$; nw–w: $r=-0.026$; $p=0.909$; w–nw: $r=-0.315$; $p=0.164$; w–w: $r=0.093$; $p=0.690$).

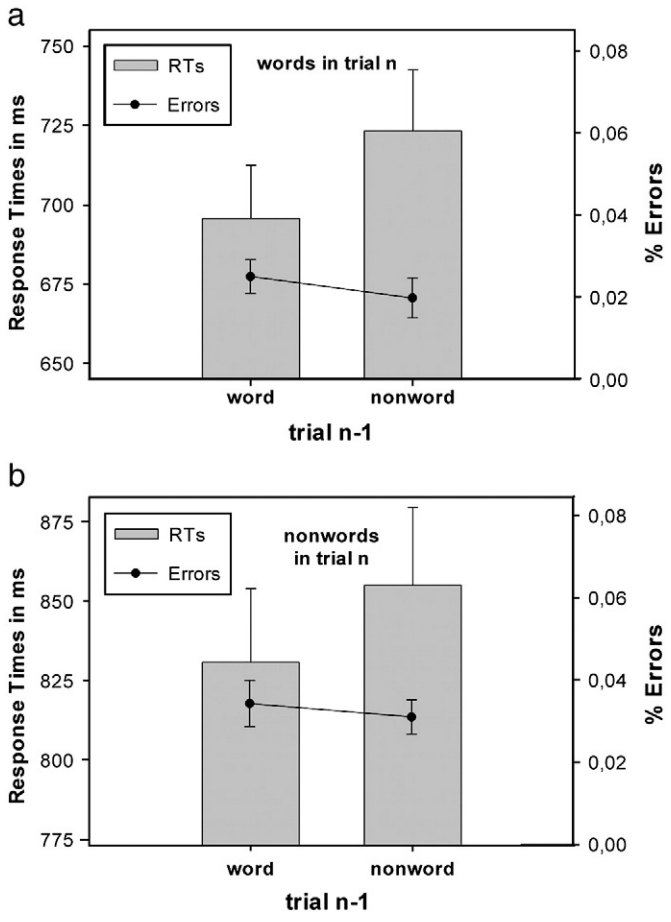

Fig. 1. Mean Response Times (in ms) and Mean Error Rates (in %) for a) current word and b) nonword trials. Error bars are standard errors of the mean.

fMRI results

Fig. 2 demonstrates that the effect of lexicality of the last trial was also mirrored in the imaging data. Irrespective of the lexical status of the current trial, processing words in the last trial elicited higher activations in the current trial in bilateral striatum (caudate and putamen), right inferior frontal cortex and bilateral middle occipital gyrus compared to the processing of nonwords in the last trial (Table 1). Neither the opposite contrast of nonword processing in the last trial nor the interaction between current and previous lexical status revealed significant effects.

The neural responses following words in the last trials were further analysed for word and nonword trials separately. For current word trials, a comparable pattern of fronto-striatal activations was visible (see Table 1). Words that were preceded by words elicited significantly more activation in left striatum compared to word trials preceded by a nonword trial. Examining current nonword trials did not reveal a significant effect at $p<0.001$. But at a slightly diminished

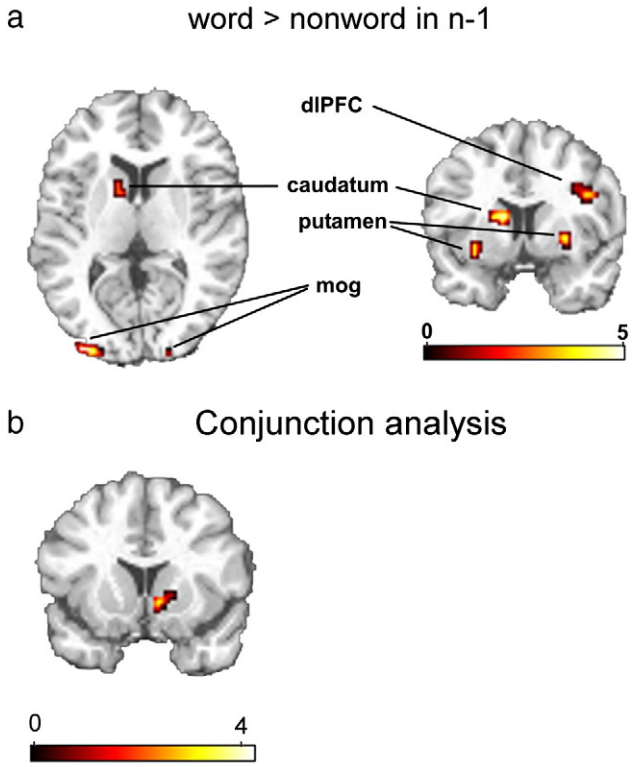

Fig. 2. a) Regions showing significantly greater activation in trials following word trials compared with trials following nonword trials. Results of the whole brain analysis overlaid on a single-subject template at $p<0.001$ (uncorr.). b) Right caudate activation revealed in a minimum statistics conjunction analysis (Nichols et al., 2005) using the response times to words and to nonwords in the previous trial as predictors of the activation in the current trial. Conjunction analysis was conducted at the second level. At the first level, onsets of the trials preceded by words, previous word trials' response times as parametric modulators, onsets of the trials preceded by nonwords, previous nonword trials' response times as parametric modulators, and onsets of the rest category, convolved with a hemodynamic response function were entered into a GLM. Simple t-contrasts of the two parametric modulators were subjected to an ANOVA at the second level, using nonsphericity correction. Minimum statistics conjunction analysis was used to reveal brain areas activated by both parametric modulators. dlPFC: dorsolateral prefrontal cortex, mog: middle occipital gyrus; w–w: word–word sequence; nw–w: nonword–word sequence; w–nw: word–nonword sequence; nw–nw: nonword–nonword sequence.

Table 1
Regions showing significant activations related to words in the last trial compared to nonwords in the last trials (MNI coordinates) at p<0.001 (uncorr.).

	# voxel	X	Y	Z	t-value
Region					
Right inferior frontal gyrus	23	42	7	25	4.88
Left caudate	25	−12	9	13	4.64
Right putamen	24	30	6	−3	4.24
Left putamen	17	−30	5	−8	4.19
Left middle occipital gyrus	19	−36	−93	10	5.01
Right middle occipital gyrus	22	21	−95	16	4.98
Words only: w–w>nw–w					
Right middle frontal gyrus	240	45	30	18	5.34
Right inferior frontal gyrus	32	39	7	30	4.90
Right precentral gyrus	16	42	−18	53	4.61
Left caudate	90	−15	6	11	4.79
Left medial wall	18	−6	−24	54	4.54
left inferior frontal gyrus	13	−50	21	21	4.38
Right middle occipital gyrus	48	42	−82	15	5.11
Right thalamus	15	6	−12	1	4.75
Nonwords only: w–nw>nw–nw					
Right caudate	19	12	20	2	3.79*
Left superior frontal gyrus	14	−24	−8	64	3.53*
Conjunction analysis					
Right caudate	12	9	11	−6	3.64
Left rectal gyrus	13	−6	37	−22	4.21
Left medial frontal gyrus	27	0	52	−8	4.02
Left posterior cingulate gyrus	53	−3	−57	24	3.80
Right precuneus	11	15	−60	25	3.73

* p<0.005 (uncorrected).

significant threshold of p<0.005 (k≥10) an activation of the right caudate and the left superior frontal gyrus was visible for nonword trials that were preceded by words.

A conjunction analysis was performed to further elaborate the relationship between criterion setting and striatal activation. If a criterion adaptation occurs following easy to process trials, such as proposed by Taylor and Lupker (2001), the striatal activation should be directly linked to the difficulty of processing during the last trial — independent of whether a word or a nonword was processed. Therefore, we examined a minimum statistics conjunction analysis (Nichols et al., 2005) using the response times to words and to nonwords in the previous trial as predictors of the activation in the current trial. Task difficulty in the LDT can be interpreted in terms of shorter response times. Hence, a negative correlation between the response times in the previous trial and the current trial's brain activation should reveal regions that are more activated the more easy to process the last trial was, thus leading to a lowering of the response criterion. Accordingly, the conjunction of both regressors revealed a negative correlation between right caudate activations and responses times to words and nonwords in the previous trial (see Fig. 2b), indicating that facilitated processing of words and nonwords in the previous trial is associated with current higher activation in right caudate (Table 1).

Discussion

This study tested the hypothesis that the basal ganglia, and in particular the striatum, are involved in decision criteria processing in higher cognitive tasks. Using the lexical decision paradigm of visual word recognition, we contrasted the activation in word–word and word–nonword trial sequences with nonword–word and nonword–nonword sequences to reveal the neural basis of sequential dependencies. The behavioural data replicate the known pattern that subjects responded faster to trials following word stimuli as compared with trials following nonwords, indicating that subjects adapt their response criterion on a trial-by-trial basis.

Furthermore, in accordance with previous studies, the error data did not show a significant effect (Lima and Huntsman, 1997; Perea and Carreiras, 2003, see Taylor and Lupker, 2001, Fig. 3 for a discussion of a non-linear relationship between response times and errors to explain the effect), although higher correlations between errors and response times occurred following word trials. Thus, the response times might indicate a speed-accuracy trade-off, though the effect was relatively weak in the error data. Still, the behavioural data support the idea that in a task like the LDT subjects use the strategy to adapt their response criterion following easy to process word trials (resulting in a reduction of response times), while at the same time they are able to achieve an acceptable level of accuracy without increasing the overall error rate.

The present imaging data also show that these sequential effects in the lexical decision task are associated with striatal activations. More importantly, the observed striatal activation is not related to error processing, because error trials and the trials following error trials were excluded from all analyses. Striatal activation following word trials was visible in both conditions, when the current trial is a word and when the current trial is a nonword. We argue that these imaging results are best explained by the effect that the previous trial has on the processing of the current trial, which is associated with strategic shifting of the response criterion by the subjects.

Taylor and Lupker (2001) summarized the behavioural findings of different n choice tasks and suggested that a common principle of these tasks is that the context of a situation affects the setting of the response criterion (e.g. Treisman and Williams, 1984, see Taylor and Lupker, 2001, p. 129 for a discussion). In the light of the LDT, context is defined as the presence of a word in the previous trial. Hence, response criterion setting can be thought of as a two-component process. In a first step, subjects place a response criterion to follow the task instructions. This criterion is then adjusted on the basis of feedback from each trial. Positive contextual feedback, the detection of a word in the previous trial, leads to decrease in criterion and negative feedback to an increased criterion (Taylor and Lupker, 2001). In visual word recognition the result of this adjustment is on average slightly faster responding following word trials (Taylor and Lupker, 2001).

The present functional imaging results are thus consistent with theories that propose basal ganglia involvement during simple two choice tasks to compute the optimal decision criterion for maximizing the rate of receiving rewards for correct choices (Bogacz, 2007). Such models see a central function of the striatum in decision making and action selection, and can account for a broader range of data like the role of the basal ganglia in reinforcement learning (Bogacz, 2007) and processing of reward-related signals (Lo and Wang, 2006). A role of the striatum in decision criterion adjustment has been proposed by a recent fMRI study using a simple perceptual two choice paradigm (Forstmann et al., 2008). These data emphasize a relationship between striatum activation and response criterion setting by showing that subjects' individual, model estimated response setting parameter varied significantly with the activation changes in the striatum. Although the Forstmann et al. study also examined response criterion setting under the conditions of a speed-accuracy trade-off (also Ivanoff et al., 2008), the present results extend these recent findings of decision criterion adjustment in perceptual two choice decision tasks to higher level decision making like it is present in the LDT.

Moreover, using a conjunction analysis, we were able to show a direct relation between task difficulty in the previous trial and current activation in the right caudate in both, the processing of words and nonwords in the previous trial. Thus, the present results do not only emphasize a role of the striatum in criterion setting under contextually driven decision situations. They also underline that the criterion seems to be related to an easy-to-process previous trial (Mozer et al., 2007; Taylor and Lupker, 2001). Hence, from the present

data it seems more likely that striatal activation is inversely related to the decision criterion, with higher activations following easy-to-process trials associated with a lowering of the response criterion.

Still, it should be noted that in the present study the role of the striatum cannot solely be explained in terms of action selection and suppression of competing response alternatives (Grillner et al, 2005; Redgrave et al., 1999). Both response alternatives in the current trial (a word and a nonword response) are equally probable and the striatal response is independent of both the current lexical status and the response in the current trial. Only when positive contextual information is given, like following word trials in the previous trial, a striatal activation was observable. We propose that the prefrontal activations are related to the active maintenance of contextual information (see Braver and Barch, 2002), whereas the striatal activation is best explained by trial-by-trial adaptations that do not prefer a specific response alternative in the current trial. Braver and Barch proposed that the active maintenance of contextual information in the dorsolateral prefrontal cortex leads to proactive control processes for future trials, which is supposed to be mediated by the dopaminergic system. Because the dopaminergic system is closely associated with basal ganglia functioning, we propose that the present striatal activation reflects a proactive control depending on the outcome of the frontal processing loops. Hence, top down processing elicits strategic shifts or criterion settings that are processed in the basal ganglia (e.g. Braver and Barch, 2002; Gold and Shadlen, 2007).

In language processing, the basal ganglia structures are usually associated with motor control (Lieberman, 2001), and syntax processing (Friederici and Kotz, 2003; Schirmer, 2004). Crosson et al. (2003, 2007) suggest a central role of the striatum in supporting semantic processing via intentionally guided attention, but not semantic function per se. Although we used verbal stimuli, we face problems in linking the present data to semantic processing. Subjects do not have to process the meaning of a word to correctly respond in the lexical decision paradigm (Grainger and Jacobs, 1996). Whereas this fact does not exclude subjects from activating a word's semantics, it seems unlikely that the observed basal ganglia activation can be attributed to long-lasting semantic activation of words until the next trial. Striatal activations in the present study were present in both conditions, for (w–w) sequences compared with (nw–w) sequences and for (w–nw) sequences contrasted with (nw–nw) sequences, both levels of comparisons showing a similar level of semantic activation for the contrasted conditions. Especially, the caudate activation for the w–nw>nw–nw contrast can hardly be explained by sustained semantic activation interaction with the semantic features of the current trial. Furthermore, also on a model-theoretical level, these trial-outlasting semantic effects could not account for the observed enhancement in response times in current nonword trials, because, according to recent computational models of visual word recognition, higher basal activation in nonword trials due to sustained word activation would make it more difficult to correctly reject the nonword stimulus. Instead, such sustained activation would predict generally increased response times to nonwords following word trials (Coltheart et al., 2001; Grainger and Jacobs, 1996) which is not observed in the present data. These models of visual word recognition assume that nonword responses are elicited via a flexible temporal deadline that is increased if a trial shows high levels of lexico-semantic activation. Hence, sustained activation of the previous word trial would further increase this temporal deadline, leading to increased RTs in current nonword trials. Here, indeed, we also found decreased RTs in nonword trials following word trials, a finding which does not support the semantic activation hypothesis.

Moreover, Friederici (2006) suggests that the caudate nucleus "activates when the language processing system cannot rely entirely on automatic mechanisms but has to recruit controlled processes as well". Anatomically and functionally, the striatum is connected to prefrontal regions via frontal–striatal–thalamic loops (Alexander et al., 1986; Crosson et al., 2007; Friederici, 2006; Jüptner and Weiller, 1998) explaining the close relationship between contextual top down signals from prefrontal regions to the proposed fine grained criterion tuning steps in striatal regions also in lexico-semantic processing.

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2010.08.062.

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