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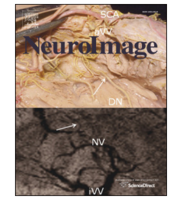

Dorsomedial striatum involvement in regulating conflict between current and presumed outcomes

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A B S T R A C T

The balance between automatic and controlled processing is essential to human flexible but optimal behavior. On the one hand, the automation of habitual behavior and processing is indispensable, and, on the other hand, strategic processing is needed in light of unexpected, conflicting, or new situations. Using ultra-high-field high-resolution functional magnetic resonance imaging (7 T-fMRI), the present study examined the role of subcortical structures in mediating this balance. Participants were asked to judge the congruency of sentences containing a semantically ambiguous or unambiguous word. Ambiguous sentences had three possible resolutions: dominant meaning, subordinate meaning, and incongruent. The dominant interpretation represents the most habitual response, whereas both the subordinate and incongruent options clash with this automatic response, and, hence, require cognitive control. Moreover, the subordinate resolution entails a less expected but correct outcome, while the incongruent condition is simply wrong. The current results reveal the involvement of the anterior dorsomedial striatum in modulating and resolving conflict between actual and expected outcomes, and highlight the importance of cortical and subcortical cooperation in this process.

Introduction

It is well-established that the prefrontal cortex supports executive functions, and that it has a compelling function in cognitive control (e.g., Badre, 2008; Koechlin et al., 2003; Miller and Cohen, 2001). Furthermore, topographically and functionally organized projections from different cortical regions to the striatum are well described and established both in human and nonhuman primates (Draganski et al., 2008; Haber, 2003; Haber et al., 2006; Kemp and Powell, 1970; Middleton and Strick, 2000; Parent and Hazrati, 1995; Selemon and Goldman-Rakic, 1985; Yeterian and Pandya, 1991; Yeterian and Van Hoesen, 1978). Cortical and subcortical regions interact with each other through these projections, which give rise to many parallel cortico-striatal-thalamo-cortical loops (Haber, 2003). Hence, owing to these extensive inputs from almost every cortical region to the striatum, the basal ganglia are considered to have a modulatory function, which complements that from the cortical regions it receives projections from, particularly by modulating, selecting, gating, and controlling the information flow (Bar-Gad et al., 2003; Frank et al., 2001; Houk and Wise, 1995). Consequently, one could hypothesize that subcortical regions, which receive inputs and form processing loops with lateral prefrontal cortex are involved in implementing cognitive control mechanisms, that is, aid cortex in light of a mismatch between what is expected and actual incoming information.

The principal aim of this research is to directly test the involvement of the basal ganglia in modulating this aforementioned form of mismatch and its resolution. We advocate a general mechanism based on probabilistic inference and probability distributions within a Bayesian framework. In short, given the evidence (in our particular case prior knowledge of relative frequency) a probability for each outcome (i.e. interpretation) is computed and the different probabilities of occurrence are ranked. Cognitive control mechanisms are required when upcoming information clashes with a so far favored (high-ranking) interpretation. In a similar vein, more than a decade ago, Jurafsky (1996) formalized a probabilistic model of sentence processing; and crucially, Pouget et al. (2013) recently proposed that a probabilistic mechanism is at the core of neural computation, and this general probabilistic approach characterizes all levels of sensory and cognitive processing. The fundamental working hypothesis is that the basal ganglia play a critical role when stimulus incompatibility with probabilistic expectations creates a conflict, which in turn, requires the engagement of cognitive control mechanisms to: inhibit a prevalent response, implement retrospective reevaluation in search of the origin of conflict and a solution, and if

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possible discharge an alternative that solves it. In this context, conflict can be manipulated by using incorrect and ambiguous sentence stimuli. While ambiguous stimuli create a conflict but at the same time provide a resolution by means of a less common but meaningful option, incorrect stimuli are simply wrong, and do not supply an alternative, which could render stimuli meaningful. This hypothesis was tested in a series of two experiments: Mestres-Misse et al. (2012) investigated structural ambiguity, that is, the same sequence could be interpreted as having two different structures (syntactic ambiguity); the present investigation focuses on local ambiguity, that is, while the structure stays the same, individual elements can have more than one meaning (semantic ambiguity).

Mestres-Misse et al. (2012) reported a rostro-caudal gradient of cognitive control within the dorsomedial striatum mirroring the described anterior–posterior cognitive control hierarchy in prefrontal cortex (Badre, 2008; Badre and D'Esposito, 2009; Koechlin et al., 2003). More specifically, in Mestres-Misse et al. (2012) both structural errors and ambiguities elicited activation in the posterior dorsomedial striatum compared to correct unambiguous conditions, but only ambiguous conditions showed activation in a more anterior dorsomedial striatal region. Taken together, these studies reflect on how the human brain accommodated to the evolutionary need of increasingly complex hierarchical control, manifested in a prefrontal posterior-to-anterior control hierarchy, which has been shown to be mirrored in the striatum.

In the present investigation, local ambiguity processing was studied by means of semantic ambiguities. In comparison to syntactic ambiguity, which depends on the relation between different elements of a sentence, semantic ambiguity is intrinsic to a particular word that has two or more meanings. In the semantic case, ambiguity resolves towards one of the meanings of a particular word, in the syntactic case, the ambiguity resolves towards one of the structures that forms a sequence of words or elements. The working hypothesis is that the basal ganglia involvement in cognitive control does not stem from increasing complexity in the coordination of different elements in a sequence, but from regulating a conflict between current and expected outcomes, which requires inhibiting an automatic, most prominent interpretation, and releasing a less common, but more relevant one.

Material and methods

Participants

Twenty-three right-handed native German speakers (11 females, mean age 26 ± 3, range 20–32) without any history of neurological or psychiatric disease participated in the current study after giving informed consent. The study was approved by the research ethical committee of the University of Leipzig.

Experimental paradigm

While in the scanner participants silently read sentences presented word by word. Their task was to judge the congruency of each presented sentence by a button-press. The experiment featured three critical ambiguous sentence conditions, namely, dominant (Dom), subordinate (Sub), and incongruent (AI). Sentences were built using unbalanced homonyms (words spelled and pronounced alike but different in meaning) with a common dominant meaning and a less common subordinate meaning (frequency-based meaning dominance). The last word of the sentence provided a biasing context (see examples below with literal English translation in brackets), supporting either the most frequent dominant (1a), or less frequent subordinate (1b) interpretation of the ambiguous word, or an incongruent context (1c).

(1a, Dom) Der *Ball* wurde von Thomas *geworfen (The ball was by Thomas thrown)*

(1b, Sub) Der *Ball* wurde von Thomas *eröffnet (The ball was by Thomas opened)*

(1c, AI) Der *Ball* wurde von Thomas *gelesen (The ball was by Thomas read)*

Furthermore, the experiment included control congruent (2a) and incongruent (2b) unambiguous (UnA) sentences.

(2a, UnAC) Das *Gras* wurde von Sarah *gemäht* (*The grass was by Sarah mowed*)

(2b, UnAI) Das *Gras* wurde von Sarah *gefragt* (*The grass was by Sarah asked*)

The target words consisted of 80 ambiguous and 80 unambiguous words (experimental materials were adapted from Gunter et al., 2003; Wagner, 2003; Wagner and Gunter, 2004). For each ambiguous word three different sentences were created, one resolving towards the more typical dominant meaning, one resolving towards the less probable subordinate meaning, and an incongruent one. For each unambiguous word a congruent and an incongruent sentence were created. In order to minimize possible differences due to phrase construction, sentences were systematically rotated across the different conditions within each word type by creating different sentence lists. Sentences were in passive voice and uniformly had a length of 6 words. Each sentence started with an article followed by the target word; subsequently, a neutral context was presented after which the disambiguating/incongruent verb (congruent with the target word for UnAC) appeared (article + target word + auxiliary verb + preposition + proper name + verb). Four lists of 160 sentences were created. Each list comprised 40 dominant (Dom) meaning sentences, 40 subordinate (Sub) meaning sentences and 80 unambiguous (UnA) sentences, which, in turn were divided into congruent and incongruent sentences, hence, 20 Dom-congruent sentences, 20 Sub-congruent sentences, 20 Dom-incongruent sentences, 20 Sub-incongruent sentences, 40 UnA-congruent and 40 UnA-incongruent. As Dom-incongruent and Sub-incongruent sentences represent the same type of context, they were collapsed into one condition (A-Incongruent, AI). The assignment of the experimental condition was systematically rotated across the four groups of 160 sentences in the four lists. Each list was divided into 4 experimental runs comprising 5 sentences per condition for Dom and Sub, and 10 for AI, UnAC and UnAI. In order to ensure that each participant saw the same ambiguous word in a dominant and a subordinate sentence context, but avoid that this occurred on the same scanning session, participants underwent two scanning sessions, one week apart. In each scanning session only one version of a given ambiguous word was presented. The order of the sessions was counterbalanced across participants. Because the principal interest of this investigation was the clash between predicted and actual outcome, Sub was considered the critical experimental condition, while Dom, AI, UnAC and UnAI represented different instances of control conditions.

Each run started with three baseline images (9 s). Each trial began with a fixation cross lasting 500 ms, then sentences were presented word by word in the center of the screen (word duration = 300 ms, SOA = 500 ms). After a variable interval between 1 and 6 s, a prompt was presented for 2 s asking participants to indicate if the sentence was congruent by pressing one of two buttons (the responding-hand was counterbalanced across participants). The screen remained dark for a variable 1- to 2-s interval. Subsequently, the next sentence was presented in the same fashion. The order of the experimental conditions within an experimental run was pseudo-randomized with the restriction that the same condition could not occur more than two times in a row. Stimulus presentation was controlled by Presentation software (Neurobehavioral Systems) and synchronized with MRI data acquisition with an accuracy of 1 ms. Stimuli were presented

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