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Research report

The impact of basal ganglia lesions on sensorimotor synchronization, spontaneous motor tempo, and the detection of tempo changes

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ABSTRACT

The basal ganglia (BG) are part of extensive subcortico-cortical circuits that are involved in a variety of motor and non-motor cognitive functions. Accumulating evidence suggests that one specific function that engages the BG and associated cortico-striato-thalamo-cortical circuitry is temporal processing, i.e., the mechanisms that underlie the encoding, decoding and evaluation of temporal relations or temporal structure. In the current study we investigated the interplay of two processes that require precise representations of temporal structure, namely the perception of an auditory pacing signal and manual motor production by means of finger tapping in a sensorimotor synchronization task. Patients with focal lesions of the BG and healthy control participants were asked to align finger taps to tone sequences that either did or did not contain a tempo acceleration or tempo deceleration at a predefined position, and to continue tapping at the final tempo after the pacing sequence had ceased. Performance in this adaptive synchronization-continuation paradigm differed between the two groups. Selective damage to the BG affected the abilities to detect tempo changes and to perform attention-dependent error correction, particularly in response to tempo decelerations. An additional assessment of preferred spontaneous, i.e., unpaced but regular, production rates yielded more heterogeneous results in the patient group. Together these findings provide evidence for less efficient processing in the perception and the production of temporal structure in patients with focal BG lesions. The results also support the functional role of the BG system in attention-dependent temporal processing.

1. Introduction

Individuals continuously adjust their behavior to environmental changes. The underlying adaptive process unfolds in time and involves the cyclic processing of motor and sensory information [1]. The question arises whether this cyclic processing is merely intrinsically temporal or to what extent temporal information is actually processed and used as a source of information in itself. Some internal representation of temporal structure is a prerequisite for efficient timing, which in turn bears the potential to optimize adaptive processes. Efficient timing of behavior implies temporally appropriate reactive and proactive actions. The latter depend on anticipation and predictions about the temporal structure of future changes or events as well as the ability to temporally align behavior with these events. Both aspects converge in sensorimotor synchronization (SMS).

SMS is a specific form of adaptive interaction with the environment. It is an extensively studied process that merges motor and non-motor components in a single setting. SMS can be characterized as the temporal coordination of a motor rhythm with an external rhythm (for reviews see [2,3]). This temporal coordination can be conceived as synchronization. Synchronization denotes the "adjustment of rhythms of oscillating objects due to their weak interaction" [4]. An oscillation is defined by its phase, relative to another oscillation, and period, and provides a means to describe the temporal relation of the events that constitute a rhythm in terms of frequency, i.e., the repetition of similar events in a specific amount of time. Complex rhythmic activity and synchronization between different rhythms constitute central aspects of life. Physiological rhythms interact continuously with each other and the environment in order to mediate between internal and external events [5]. In cognition, this implies adaptation of internally-generated to external rhythms via unidirectional coupling which eventually leads to stimulus-driven synchronization of behavior.

Both SMS and temporal processing have been modeled on the basis of oscillations and the fundamental dissociation of automatic

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and controlled sub-processes. For example, temporal processing is hypothesized to rest on the coincidental activation of medium spiny neurons in the BG by ensembles of cortical neural oscillations [6,7]. In SMS, the period of an adaptive oscillatory timekeeper is assumed to reflect the temporal structure of the pacing signal, thereby establishing a reference for the timing of successive motor commands [8]. In this context, the current study investigates a combination of these aspects by providing BG patients and controls with an oscillatory perceptual input whose temporal structure needs to be exploited to generate oscillatory motor behavior. Error correction mechanisms adjust the phase and period of the internal timekeeper oscillation if it is confronted with a perturbation, i.e., a change in the temporal structure of the pacing signal. These error correction mechanisms are dissociable based on their dependence on attention, the intention to adapt, and awareness of a tempo change [9]. Whereas phase correction depends solely on the intention to maintain synchrony and can therefore be considered automatic, period correction depends also on attention and awareness of the tempo change.

A comparable dissociation between automatic and controlled mechanisms has been proposed with respect to temporal processing [10]. More specifically, the cerebellum (CE) performs automatic or pre-attentive, short-range, event-based temporal processing, while in parallel, the BG and cortico-striato-thalamo-cortical circuitry engage in attention-dependent, longer-range, interval-based temporal processing [7,11,12]. Attention, or the ability to attentively detect a change in temporal structure may therefore not only decide upon the type of error correction, but also upon the primary temporal processing system. Temporal structure may thereby influence cognitive processes, e.g., as the basis for attentional set shifting and sequence coordination [13]. This view is consistent with Dynamic Attending Theory DAT [14], which proposes that attention can be modeled as a self-sustained oscillation capable of entrainment. Within the framework of DAT, the temporal structure of a stimulus guides the allocation of attentional resources thereby evoking stimulus-driven attending [15]. On this basis, attentive adaptation to tempo change in SMS would depend on the parallel engagement of pre-attentive and attention-dependent temporal processing systems, as well as phase and period correction to adjust internal timekeeper and/or attention oscillations.

The role of the BG in temporal processing and in SMS has been investigated primarily in patients with Parkinson's disease (PD), albeit with mixed results [16–18]. Studies involving PD patients also suggest difficulties in beat extraction and the comparison of rhythmic sequences [19]. However, PD is a progressive neurodegenerative disease, and besides medication and different PD subgroups [20] some of the heterogeneity of the respective results may be due to the variable extent of cortical damage in this population, which can be minimal or absent in patients with BG lesions [21,22]. Studies on SMS involving patients with focal lesions of the BG are scarce. Aparicio et al. [23] used a synchronization–continuation paradigm and found no evidence for impaired temporal processing performance in this group. Different tasks, stimulus characteristics, and cognitive sets add further complexity to the identification of specific BG and cerebellar temporal processing functions [24].

Besides attention, temporal range seems to be an important factor, as temporal processing evolves across different timescales that may map onto different physiological and psychological mechanisms [10,24,25]. A well-defined boundary between short-range and longer-range temporal processing remains elusive, although values around 500 ms [26] and close to 1000 ms [27] have been suggested. Fraisse [28] emphasizes that synchronization is most stable for tempi between 400 and 800 ms, while the intermediary tempo of 600 ms is most representative for unpaced, spontaneous motor activity. This has been confirmed in more recent studies [29] that also found a correlation between individual spontaneous motor tempo (SMT) and a preferred perceptual tempo [30]. It corresponds to the "indifference interval" or "indifference zone" that is neither systematically overestimated nor underestimated [28,31]. A tempo of 600 ms is within the range for optimal pulse sensation [32] and tempo sensitivity, for a review see [33,34]. Although originating from a different perspective, Karmarkar and Buonomano [35] hypothesize that temporal processing between 400 and 800 ms may be accurately performed by mechanisms underlying both time perception and time estimation. Hence, the SMS task in the current study incorporated a base tempo of 600 ms and tempo changes that induced shifts relative to this base tempo. This procedure should perturb the synchronization of internal timekeeper and/or attention oscillations. We expected that damage to the cortico-striato-thalamo-cortical attention-dependent temporal processing system due to BG lesions should lead to difficulties in the evaluation of temporal structure and consequently in maintaining attentive synchrony. These difficulties should compromise the ability to detect and to assess a tempo change which should in turn lead to a lesser degree of attention-dependent period correction during SMS in the patient group, while automatic phase correction should be preserved.

We assessed SMT before and after the main SMS task to explore whether the SMT of patients with BG lesions differs from that of healthy controls and whether it would be influenced by the intervening SMS task. For example, stronger reliance on the unimpaired cerebellar short-range system in the patient group may be reflected by a preference for faster SMT rates. SMT is not constrained by simple biomechanical mechanisms [28] and in the absence of an external pacemaker it has to rely on internally generated temporal structure and simultaneous monitoring of temporal regularity. We hypothesized that faster SMT rates in the patient group could reflect stronger reliance on the unaffected cerebellar short range temporal processing system. BG lesions should compromise both the consistency of internally generated temporal structure and the monitoring process, which in turn should lead to increased tapping variability in the patient group. In general, a better understanding of these fundamental mechanisms and the way they are altered in this specific patient group is not only important for modeling the mechanisms underlying the adaptive interaction with the environment but may also be helpful in optimizing the temporal structure of compensatory strategies used in therapeutic settings.

2. Materials and methods

2.1. Participants

10 patients with focal lesions of the BG due to stroke (mean 6.2 years post lesion onset, SD = 2.5) and 10 healthy controls (one woman per group) participated in the current study. None had prior experience with finger tapping in an experimental setting. The group comprised eight patients with partial middle central artery infarction and two patients with intracerebral hemorrhage. Lesions were left-lateralized in eight, and right-lateralized in two patients. In seven patients lesions affected anterior and posterior parts of the striatum. In two patients lesions were focused in the posterior striatum, and in one patient in the anterior striatum, respectively. A structural overlay of the lesions is depicted in Fig. 1. Ages ranged from 30 to 68 years and mean age was 46.7 years (SD = 13.3). Healthy controls were recruited via the database of the Max-Planck Institute for Human Cognitive and Brain Sciences and matched the patients in terms of age, education (in years), gender and handedness. All participants received a compensatory fee and gave their informed consent before they were tested. The study was approved by the local medical ethics committee at the University of Leipzig.

2.2. Spontaneous motor tempo task

To assess the SMT of patients and controls we applied a similar procedure as McAuley and co-workers [29]. Participants were asked to tap regularly at their most comfortable rate for a short period of time. A single tone sounded after 31 taps (30 inter-tap intervals (ITI)) were recorded. No auditory feedback was given. This task was carried out before and after the main SMS task in order to test for the potential influence of this task on SMT rates.

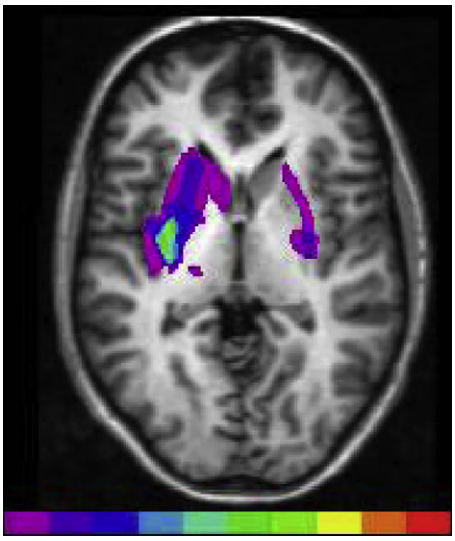

Fig. 1. Structural overlay of basal ganglia lesions. Green shades are associated with maximum lesion overlap, whereas purple shades are (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.) associated with minimal lesion overlap.

2.3. Sensorimotor synchronization task

All participants used the index finger to tap on an electronic percussion pad (Roland SPD-6) placed on a table in front of them. The pad was connected to a Windows PC via a MIDI interface. A quiet "thud" sound with intensity proportional to tapping force was produced upon impact with the rubber surface of the pad. This sound was further attenuated by the use of headphones. However, no digital sound output was provided. The manual mode of the pad was selected (as opposed to drumstick mode). Prior to the SMT and SMS tasks, all participants were allowed to familiarize themselves with the setting, and to test different styles of tapping in order to find the most comfortable tapping position. Some participants decided to tap while holding their forearm above the pad, but most preferred to rest their hand on the pad. All patients tapped with their less affected ipsilesional hand in order to reduce possible confounds of impaired motor control. Some patients reported that they had used this hand more frequently in the average 6.2 years since lesion onset. Control participants tapped with their dominant right hand. The adaptive timing task applied in this study was the same as the one used by Repp and Keller [9] with the exception that the current base tempo was 600 ms instead of 500 ms.

Stimulus presentation and tap recording was controlled by a program written in MAX (http://www.cycling74) running on a Windows PC. Stimuli were presented via headphones (Sennheiser HD 202) at a comfortable intensity. A total of 100 pseudo-randomized synchronization–continuation trials were processed in 10 blocks of 10 trials each. 10 identical high-pitched piano tones (C8; 4176 Hz) were used as pacing stimuli during the synchronization phase of each trial. In eight trials per block the initial inter-onset interval (IOI) of 600 ms was presented six times and was then followed by tempo accelerations or decelerations with a magnitude of 30, 45, 60 or 75 ms for the three remaining IOIs. Two trials per block did not contain a tempo change and served as control sequences. Thus, if the trial contained a tempo change, it occurred between the 7th and 8th tone of the pacing sequence. Participants were instructed to start tapping with the third tone of the pacing sequence. An additional single tone of lower pitch (E7) marked the end of the continuation phase and served as a signal to stop tapping. Awareness of the tempo change was assessed by means of a perceptual judgment. At the end of each trial, participants reported orally whether they had perceived a deceleration, acceleration or no tempo change within the pacing sequence. Presentation of the next trial started two seconds after the experimenter recorded the decision via key press. All data were acquired during a single session of approximately 60 min.

Missing taps and taps that either followed the target position by more than 130 ms or preceded it by more than 150 ms were excluded from the analysis and are referred to as errors. For the control sequences, mean asynchrony (MA) between taps and pacing sequence tones, variability of asynchronies, mean ITI during synchronization and continuation, and variability for ITIs produced during synchronization and continuation were calculated. Adaptation to tempo changes was assessed in terms of mean ITIs, error correction and perceptual sensitivity to tempo changes on five positions of interest (s0, s1, s2, s3, c). Position s0 corresponds to the ITI terminated by the tap that coincided approximately with the first tone at the new sequence tempo. This is followed by positions s1, s2 and s3. Position s3 thus corresponds to the ITI initiated by the tap coinciding approximately with the last sequence tone. Finally, c represents the average ITI during the whole continuation phase [9].

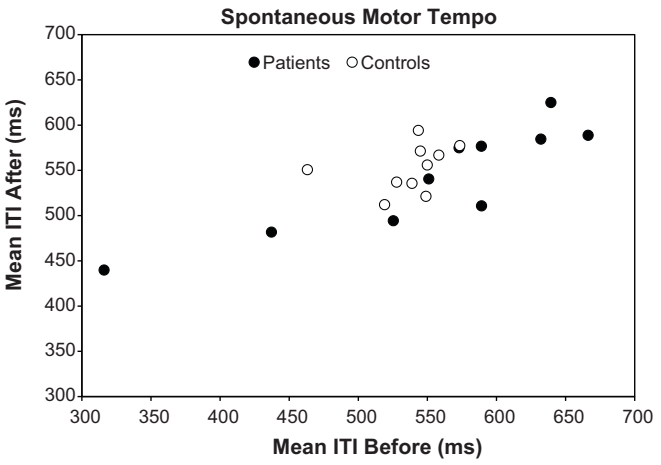

Fig. 2. Distribution of spontaneous motor tempo for patients with basal ganglia lesions and healthy controls before and after the adaptive timing task. ITI = intertap interval.

3. Results

3.1. Spontaneous motor tempo

Mean SMT in the patient group was 551 ms (SD 105 ms) before, and 541 ms (SD 58 ms) after the SMS task. For the control group the corresponding values were 536 ms (SD 30 ms) before, and 552 ms (SD 26 ms) after the SMS task (Fig. 2). Distribution of SMT rates differed between the two groups. Levene's test of equality of error variances revealed that the patient group was more heterogeneous than the control group before, $F(1.18) = 5.94$, $p < .03$, and after the SMS task, $F(1.18) = 7.64$, $p < .02$. However, contrary to our prediction there was no unitary trend towards either shorter or longer ITIs. Instead, patients demonstrated both fast and slow SMT rates, while control's SMT rates clustered around 550 ms.

SMT variability was assessed by the coefficient of variation (CV) that was computed by dividing the standard deviation of individual ITIs within a trial by the mean ITI. Tapping variability was higher in patients than in controls (Fig. 3). Furthermore, variability was generally lower after the adaptive timing task than before it. This was the case both in patients and in controls. In this case, Levene's test of equality of error variances was not significant. A 2×2 ANOVA

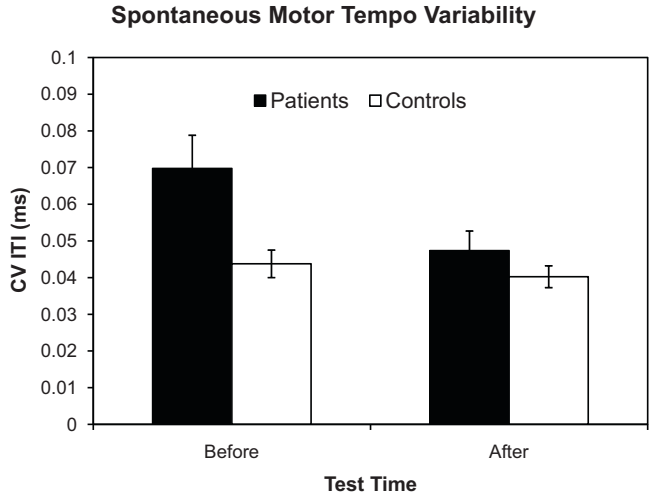

Fig. 3. Coefficients of variation (CV) for the spontaneous motor tempo task for patients with basal ganglia lesions and healthy controls before and after the adaptive timing task.

Table 1
Mean Asynchrony, mean intertap interval (ITI), and coefficient of variation (CV) of ITIs for patients and controls during synchronization and continuation.

	Mean asynchrony	CV asynchrony	Mean ITI synchronization	Mean ITI continuation	CV ITI synchronization	CV ITI continuation
Patients	−31	0.048	596	595	0.057	0.061
Controls	−26	0.034	600	598	0.041	0.044

with factors group (patients vs. controls) and test time (before vs. after the adaptive timing task) yielded significant differences for group $F(1.18) = 6.74$, $p < .02$ and test time $F(1.18) = 6.45$, $p < .03$; but no significant interaction, group × test time $F(1.18) = 3.44$, $p = .08$. These results imply more variable generation of temporal structure in the patient group.

Due to erratic performance during the subsequent SMS task one patient and the respective control had to be excluded from all further analyses except for the detection task. Exclusion of these participants changed the results of the preceding ANOVA to group $F(1.16) = 7.78$, $p < .02$; test time $F(1.16) = 4.84$, $p < .05$; and group × test time $F(1.16) = 3.84$, $p = .07$.

3.2. Adaptive timing task

For the full sample of participants, the percentage of errors was 4.5% for patients and 1.4% for controls, $t(18) = 1.90$, $p = .07$. However, one patient and the respective control were excluded from all further analyses. This patient tapped at a tempo independent of the pacing sequence tempo. Mean ITI was 497 ms for synchronization and 496 ms for continuation. The tapping was quite stable during synchronization (CV = .053) and highly stable during continuation (CV = .036). It is tempting to speculate that the tempo of the pacing sequence distracted the patient from tapping at a preferred rate (SMT before = 437 ms and SMT after = 482 ms). For the remaining participants, percentage of errors was 3.4% for patients and 1.5% for controls, $t(16) = 1.34$, $p = .16$. Results for the control sequences without a tempo change are provided in Table 1. The negative values for MA indicate that the taps preceded the pacing stimulus, which is a typical finding for SMS in inexperienced tappers [36].

While the groups did not differ with respect to MA, $t(16) = .34$, $p = .74$, the CV for asynchronies was higher for patients $t(16) = 2.36$, $p < .04$. Mean ITIs, and CVs for synchronization and continuation were analyzed in separate 2 × 2 ANOVAs to test for the effects of phase (synchronization vs. continuation) and group (patients vs. controls). The ANOVA on mean ITIs revealed no significant differences, phase $F(1.16) = .75$, $p = .40$; group $F(1.16) = .17$, $p = .69$; phase × group $F(1.16) = .02$, $p = .90$. However, the ANOVA on CV of ITIs yielded a significant effect for phase $F(1.16) = 19.25$, $p < .01$, but not for group $F(1.16) = .70$, $p = .42$, and no significant interaction phase x group $F(1.16) = .055$, $p = .82$, indicating less variability during the paced synchronization phase. Together, these results demonstrate that the patients could principally synchronize their motor behavior with the auditory pacing sequences.

To examine the adaptive response to the tempo changes, mean ITIs were plotted as a function of final sequence tempo separately for all sequences, including the control sequences, for patients and controls for each sequence position of interest (s0, s1, s2, s3, c) (Fig. 4).

Regression lines were fitted to the slopes of these ITI functions and were used as adaptation indices (Fig. 5). A value of 1 represents perfect adaptation, values less than 1 indicate undercorrection and values greater than 1 overcorrection. Adaptation indices were computed separately for tempo increases (i.e., faster tempi with final sequence IOIs < 600 ms) and tempo decreases (slower tempi with final sequence IOIs > 600 ms).

A 2 × 2 × 4 ANOVA was conducted to examine the effects of group (patients vs. controls), tempo (faster vs. slower), and position (s1, s2, s3, c) on adaptation indices. The observed adaptation indices differed between the groups $F(1.16) = 5.43$, $p < .04$ and between positions $F(3.48) = 9.32$, $p < .01$. Adaptation indices were generally higher in controls than in patients, and decreased across sequence positions in both groups. However, there were no significant interactions between group x tempo $F(1.16) = 2.97$, $p = .10$ or position × group $F(1.16) = .33$, $p = .57$. Error correction was partioned into phase correction and period correction according to the two-process model of error correction [8]. These types of error correction were estimated by determining the values of the parameters that led to the best fit between predictions based on the two-process model of error correction (implemented in MATLAB) and the observed adaptation indices [9]. Average phase and period correction estimates for tempo increases and decreases are shown separately in Fig. 6 for patients and controls. The fact that these values are higher than those observed by Repp and Keller [9] may be attributed to the participant's relative inexperience with finger tapping (Repp and Keller tested highly trained tappers) and/or the slower base tempo employed in the current study (600 ms vs. 500 ms).

Separate 2 × 2 ANOVAs, with independent variables group (patients vs. controls) and tempo (faster vs. slower), were conducted for phase and period correction. The results indicated that period correction was generally more effective at faster tempi, Tempo $F(1.16) = 8.14$, $p < .02$. However, the effects of tempo on period correction were different for patients and controls,

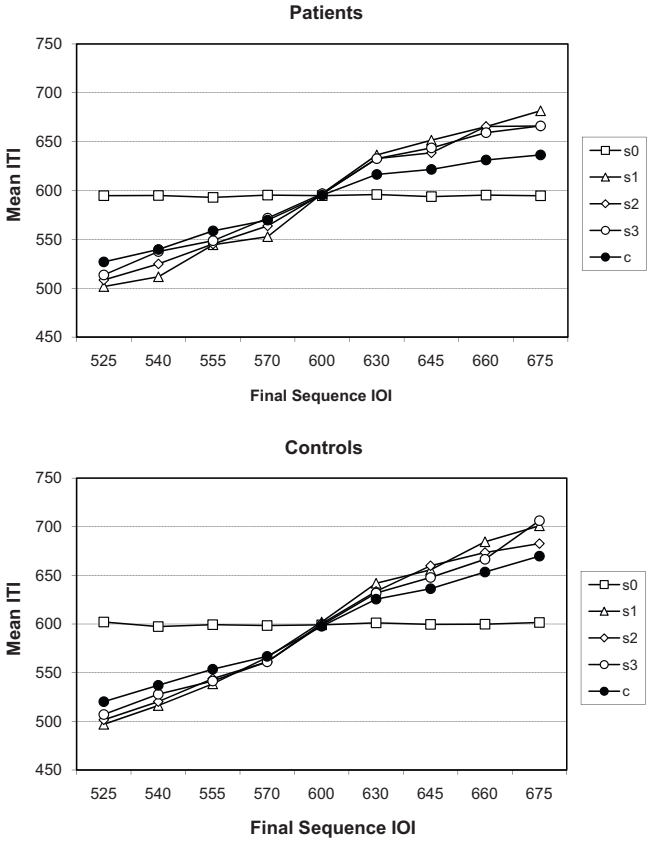

Fig. 4. Mean intertap intervals (ITI) for basal ganglia patients and healthy controls as a function of the final sequence inter-onset interval (IOI).

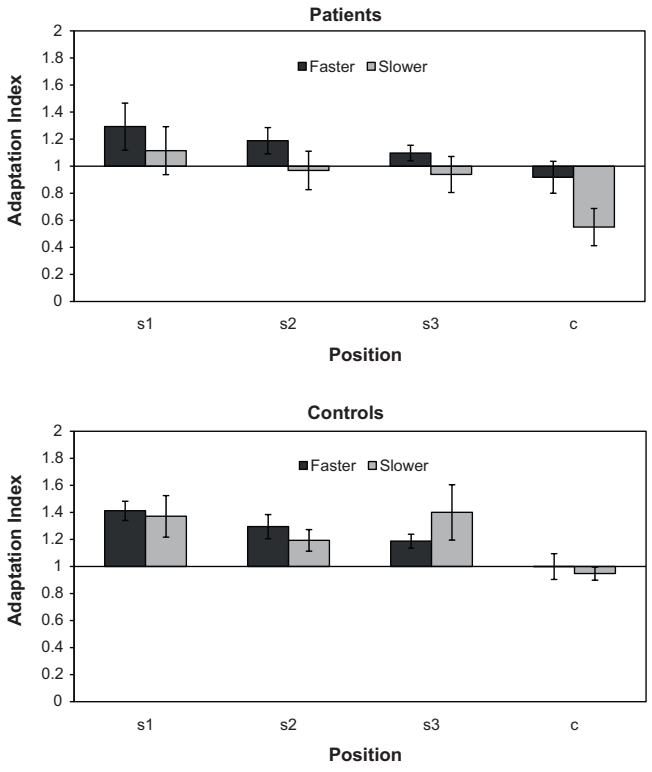

Fig. 5. Adaptation indices for basal ganglia patients and healthy controls for the sequence positions following the tempo change (s1, s2, s3) and during continuation tapping (c).

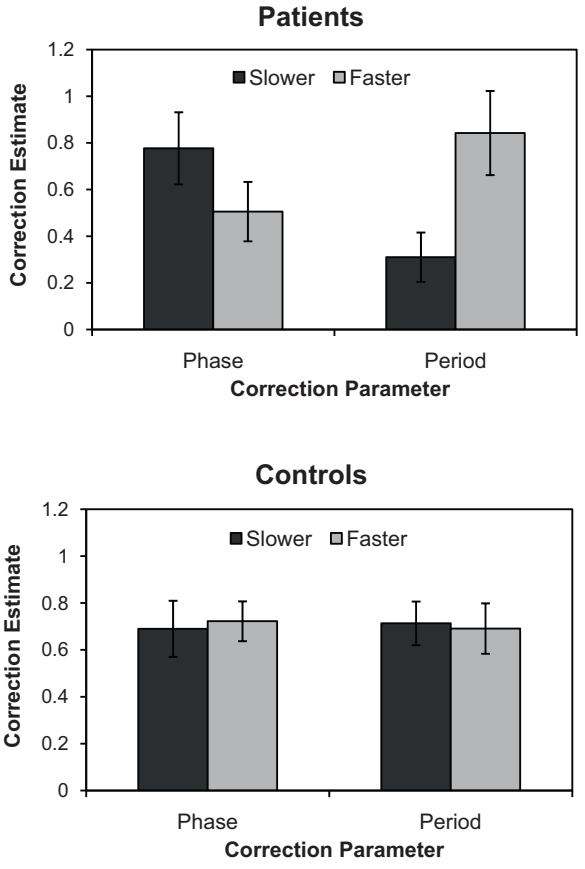

Fig. 6. Phase and period correction estimates for basal ganglia patients and healthy controls for tempo accelerations (faster) and decelerations (slower).

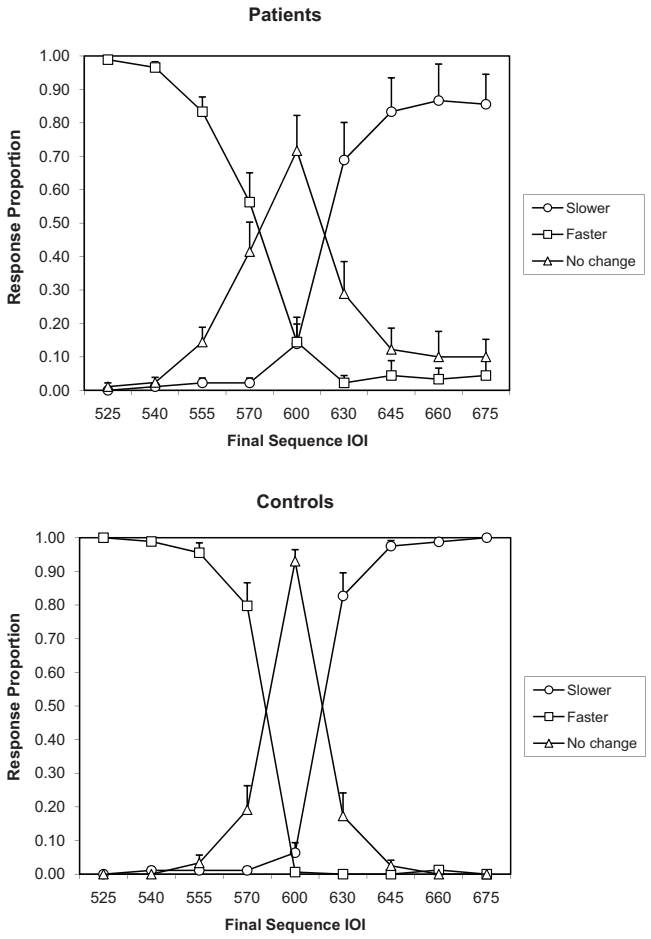

Fig. 7. Proportion of responses to tempo changes for basal ganglia patients and healthy controls. IOI = interonset interval.

group × tempo $F(1.16) = 9.625$, $p < .01$. Patients engaged in less effective period correction at slower tempi than at faster tempi, $F(1.8) = 14.52$, $p < .01$, whereas such effects of tempo on period correction were absent in controls, $F(1.8) = .40$, $p = .85$.

3.3. Detection task

At the conclusion of each synchronization-continuation trial, participants were required to indicate orally whether the pacing sequence tempo had become faster, slower, or had remained constant. Average responses are shown for both groups in Fig. 7.

The responses of all participants were converted into d′ scores in order to take potential response biases into account (Fig. 8). These scores were computed by subtracting z-transformed false alarm rates (i.e., the proportion of "slower" or "no change" responses for tempo increases, and "faster" or "no change" responses for tempo decreases) from hit rates ("faster" responses for tempo increases, and "slower" responses for tempo decreases). In accordance with our hypotheses, patients seemed to be more accurate for tempo accelerations while their performance for decelerations reached a plateau at +45 ms. A 2 × 2 × 4 ANOVA on these scores tested for the effects of group (patients vs. controls), tempo (faster vs. slower), and magnitude (±30, 45, 60, 75 ms). This ANOVA was computed for the whole sample of participants as the perceptual judgment did not involve any motor component.

A main effect of group was significant, $F(1.18) = 5.01$, $p < .04$, which confirms that patients were generally less sensitive to the tempo changes than controls. The effect of magnitude was sig-

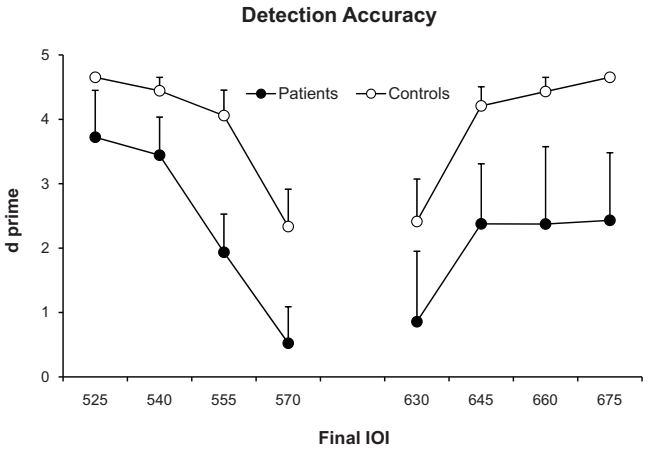

Fig. 8. Accuracy in the detection of tempo change for basal ganglia patients and healthy controls.

nificant, $F(3.48) = 8.02$, $p < .01$ and greater for accelerations than for decelerations, tempo × magnitude $F(3.48) = 21.64$, $p < .01$. There was no significant three-way interaction. Only an additional post-hoc 2 × 2 ANOVA restricted to the perceptually most salient changes (±75 ms) that should easily draw attention yielded an interaction for group × tempo, $F(1.18) = 5.45$, $p < .03$.

4. Discussion

The current study explored spontaneous motor tempo and sensorimotor synchronization in patients with focal BG lesions by means of two finger tapping tasks. Damage to the BG was associated with a more heterogeneous distribution of individual rates as well as more variable tapping during the SMT task. These results confirm that BG lesions have an effect on SMT in that they affect the ability to execute a steady sequence of periodic actions. Given the role of the BG in attention-dependent temporal processing, higher variability may be caused by imprecise representations of temporal structure. Alternatively, it could be simply due to noisy motor implementation. However, it seems unlikely that this is also the reason for the more heterogeneous distribution of SMT rates. In general, patients performed well in both tapping tasks and did not report difficulties with tapping per se. This suggests, that the freely chosen SMT rates reflect a different process. In the absence of external cues, SMT has to rely on internally generated, temporally regular pacing information. Such internal pacemaker function most likely engages the pre-supplementary motor area (pre-SMA) and its connections to the BG. The pre-SMA contributes to the planning and initiation of simple and complex action sequences, including those required during speech production [37]. Pre-SMA recruitment is strongest when actions are freely chosen and are not guided by external signals [38,39], with increased activation in early PD patients [40]. However, the pre-SMA is also involved in perceptual temporal processing [41,42], indicating a function in production and perception. Hence, heterogeneous SMT rates and higher variability can be explained on a structural level by impaired processing of temporal structure in connections from the pre-SMA to the anterior striatum [43,44], the site affected in most patients.

Patients demonstrated good overall performance during SMS, however, they tapped with relatively high variability and their error correction was affected. More specifically, attention-dependent period correction was less efficient in response to tempo decelerations. Again, higher variability may be due to noisy motor implementation, whereas the difference in error correction hints at another process. While any specific value such as the 600 ms tempo used in the current study is certainly too precise to dissociate short-range from longer-range temporal processing, tempo changes relative to this base tempo were sufficient to induce a distinct impairment in the patient group. The fact that period correction was affected supports the notion of specific attention-dependent mechanisms underlying SMS and temporal processing. This process may be modeled as entrainment of the timekeeper and/or attention oscillation by a pulse train [4]. Whereas phase correction would be sufficient to compensate for subliminal perturbations encoded by the pre-attentive temporal processing system, additional period correction would be needed to adapt if the period of the internal timekeeper has to be adjusted. In the absence of subdivisions, that is, in the context of 1:1 tapping [45], phase correction is assumed to reflect a lower-level process and to rest on times of occurrence or reference points, whereas period correction is assumed to rest on intervals and to involve some form of memory for at least one preceding event. Based on EEG data, Praamstra et al. [46] localized period correction in the supplementary motor area (SMA). The finding of impaired period correction is thus in line with the proposed role of the BG in interval-based, longer range temporal processing and an ongoing evaluation of temporal structure in cortico-striato-thalamo-cortical circuits involving the pre-SMA.

The periodically spaced events of the pacing sequence promote stimulus-driven synchronization. However, if attention-dependent temporal processing is necessary to recognize temporal regularity, BG lesions could be responsible for an erratic evaluation of temporal structure and inaccurate predictions about upcoming events. In line with DAT, this should affect the ability to focus attention in time and to detect a tempo change. In other words, while the temporal structure of successive pacing events conveys regular temporal structure that is precisely encoded by the pre-attentive temporal processing system, its potentially facilitatory effect on synchronization is weakened by inefficient attention-dependent temporal processing. This relates to the difficulties of PD patients in processing rhythms with a beat structure [19] and evidence for difficulties in temporal preparation in contrast to intact encoding of temporal intervals [47]. Damage to the BG may affect the ability to evaluate the temporal relations between successive events, thereby compromising the use of this information to compare rhythms, to align motor behavior, or to allocate attention. The detection of a subsequent event may then be affected by both imprecise representation and evaluation of temporal structure on the one hand and inefficient allocation of attention in time on the other hand. This in turn may explain the difficulties that patients displayed in detecting the tempo changes embedded at a predictable position in the pacing sequences.

The results of the present study speak in favor of a function of the BG in SMS that is not restricted to motor control, but that extends to attention-dependent temporal processing. Temporal processing and the recognition of temporal regularity are crucial for anticipation, which in turn is necessary to temporally align actions to events in the environment. The additional finding of reduced perceptual sensitivity to tempo changes in BG patients points to a temporal processing network that is engaged in both production and perception. Together, attention-dependent temporal processing and resulting difficulties to exploit temporal structure in stimulus-driven attending and adaptive motor control offer an explanation for the observed differences between patients with BG lesions and healthy controls.

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