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Abstract

The striatum, the largest component of the basal ganglia, is usually subdivided into associative, motor and limbic components. However, the electrophysiological interactions between these three subsystems during behavior remain largely unknown. We hypothesized that the striatum might be particularly active during exploratory behavior, which is presumably associated with increased attention. We investigated the modulation of local field potentials (LFPs) in the striatum during attentive wakefulness in freely moving rats. To this end, we implanted microelectrodes into different parts of the striatum of Wistar rats, as well as into the motor, associative and limbic cortices. We then used electromyograms to identify motor activity and analyzed the instantaneous frequency, power spectra and partial directed coherence during exploratory behavior. We observed fine modulation in the theta frequency range of striatal LFPs in 92.5 ± 2.5% of all epochs of exploratory behavior. Concomitantly, the theta power spectrum increased in all striatal channels (P < 0.001), and coherence analysis revealed strong connectivity (coefficients >0.7) between the primary motor cortex and the rostral part of the caudatoputamen nucleus, as well as among all striatal channels (P < 0.001). Conclusively, we observed a pattern of strong theta band activation in the entire striatum during attentive wakefulness, as well as a strong coherence between the motor cortex and the entire striatum. We suggest that this activation reflects the integration of motor, cognitive and limbic systems during attentive wakefulness.

Key words: Attention; Behavior; Striatum; Theta rhythm; Partial directed coherence

Introduction

Lesions in the basal ganglia are known to promote severe motor disturbances. Unilateral depletion of striatal dopamine in rats, for example, causes ipsilateral rotation (1), clumsy and inefficient use of the contralateral paw (2-4), and also failure to respond adequately to stimuli to the contralateral side, a phenomenon called "striatal neglect" (5). Moreover, the striatum, the largest component of the basal ganglia, is known to be involved in mental activities other than movement control. Corroborating these functional observations, anatomical studies (6-8) divided the striatum of rodents into 3 main parts, based on their connectivity pattern: 1) a limbic region (9,10) in the ventromedial striatum (in the context of "expanded amygdala" and the ventral striatopallidal system), which is connected to the orbitofrontal and cingulate cortical areas and is responsible for motivational and reward processing; 2) a motor region

(11,12), which is centered around the putamen, and is closely connected to the sensorimotor cortex, and 3) an associative region (13) in the dorsolateral striatum, which is connected to the prefrontal cortical area and is involved in cognitive processing. Moreover, histological studies using multiple fluorescence have demonstrated additional subdivisions based on the neurotransmitters expressed (14). Nevertheless, the functional significance of these anatomical divisions still remains to be determined.

Oscillations are a key mechanism of dynamic coupling between brain areas, and local field potentials (LFP) are modulated by task- and state-dependent changes (15). Theta oscillations (5 to 11 Hz), particularly, are commonly observed during the activation of numerous brain structures. The theta rhythm is related to learning, attention and memory tasks (16), facilitates synaptic plasticity (17),

influences reaction time (18), and correlates with increased attention (19).

The theta rhythm is a prominent feature of hippocampal spike and local field potential activity in rats, and has been recorded while animals engage in active behaviors (20-22). Other studies have observed theta activity in other cortical and subcortical regions, including the striatum (21). Nevertheless, some investigators have reported the occurrence of hippocampus-coherent theta in limbic portions of the striatum (23,24), and defend the notion that striatal theta is not locally generated, but recorded due to volume conduction from the hippocampus (i.e., electrotonic spread of current).

Here we asked whether the striatal theta rhythm is modulated during spontaneous behavior in rats. To do this, we recorded LFP in associative, limbic and motor areas of the caudatoputamen complex of rats while the animals a) rested or b) actively explored their environment; during exploration, it is reasonable to assume that a higher degree of attention is required. We found that striatal LFP activity modulates in the theta band during exploratory behavior, and oscillates in strong coherence (highly synchronous) with the theta rhythm in the primary motor cortex. This striatal activity was not coherent with hippocampal theta, and thus cannot be explained by volume conduction from the hippocampus, indicating that it might be locally generated. We suggest that such rhythmic activity most likely influences attention processing in neocortical areas, and that the striatum therefore plays a central role in the integration of associative, limbic and motor systems during attentive wakefulness.

Material and Methods

Methods

Seven adult Wistar rats of both sexes, weighing 270 to 310 g (corresponding to 2-3 months of age depending on the sex), were anesthetized with an intraperitoneal injection of diazepam, 0.5 mg/100 g, and ketamine, 10 mg/100 g (Merck, Germany) in accordance with the national and institutional guidelines for animal experimentation, after approval by the Research Ethics Committee of Universidade de São Paulo, as well as with the National Institute of Health Guide for the Care and Use of Laboratory Animals (NIH Publications No. 80-23 from 1996). The surgical procedure was described elsewhere (25). Bipolar nickel-chrome

electrodes (wire thickness 120 µm) were previously set up with active contacts 300 µm apart. The animals were then secured to a Cunningham stereotactic frame (Stoelting Co., USA). According to previously determined stereotactic coordinates from the Paxinos' atlas (26) for the deep targets and Zilles' atlas (27) for cortical ones, bipolar surface electrodes were placed over cortical areas 10 (prefrontal, AP = 4.0; L = 2.0), 6 (sensorimotor, AP = -2.7; L = 3.2), 17 (visual, AP = -7.3; L = 4.0). Deep bipolar electrodes were inserted into Ammon's horn 3 of the hippocampal formation (CA3, AP = -2.3; L = 1.5; H = 3.5), and additionally into five different portions of the caudatoputamen complex as follows: rostral (CPur, AP = 1.7; L = 2.5; H = 5.0), dorsolateral (CPudl, AP = -0.8; L = 4.0; H = 3.8), ventral (CPuv, AP = -0.8; L = 4.0; H = 5.8), medial (CPum, AP = -0.8; L = 2.5; H = 4.5), and caudal (CPuc, AP = -1.8; L = 4.5; H = 5.0), as illustrated in Figure 1. In addition, bipolar electrodes
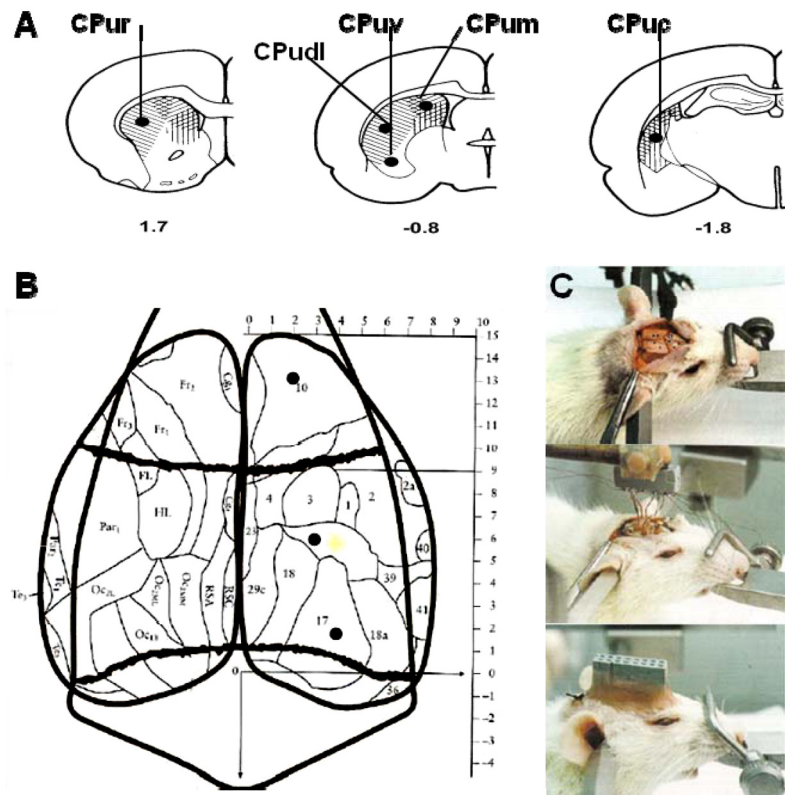

Figure 1. Implantation technique. *A*, Target coordinates in the striatum according to the Paxinos atlas: CPur denotes the rostral part, CPudl the dorsolateral part, CPuv the ventral, CPum the medial part, and finally CPuc the caudal part of the caudate putamen. *B*, Coordinates of the cortical electrodes according to Krieg's atlas (on the right); the functional atlas of Zilles is represented on the left side for orientation. The cortical areas A10 (prefrontal), A6 (sensorimotor), A17 (visual), and hippocampal Ammon's horn CA3 were bilaterally implanted to allow definition of the sleep-wake cycle and alertness degree. Additional bipolar electrodes in the neck musculature, eyes and vibrissae allowed categorization of the movement pattern. *C,* Stereotactic procedure for implantation of the surface and deep brain electrodes.

were inserted into the neck muscles, eyes and vibrissae to monitor the movement pattern. Electrodes were then fixed to the skull with methyl methacrylate and coupled to an electrical interface for later recording. Recordings were performed by transferring the animals at night to a recording chamber, and connecting them to a computer interface wired-linked to a Nihon-Kohden electroencephalograph (Neurofax EEG-5532, Japan). Signals were filtered with a band-pass filter fom 1 to 475 Hz and recorded on a personal computer via an analog-digital converter (CED, Cambridge Electronic Design Ltd., UK) at a 1-KHz sampling rate for off-line analysis. The potentials were analyzed both visually (for characterization of behavioral patterns) and instrumentally as described below. The mathematical analyses used here were developed by Prof. K. Sameshima in our laboratory (Universidade de São Paulo) for the Matlab® environment (Mathworks Inc., USA). Animals were observed during their sleep-wake cycles and all episodes of wakefulness lasting longer than 10 min were visually selected based on motor activity, as well as predominance of desynchronization in the prefrontal cortex. These episodes included periods of rest wakefulness, during which animals were quiet or walking slowly in their cages. Next, we selected within these longer episodes of wakefulness, the first 6 periods of attentive wakefulness per animal (a total of 42 epochs), lasting 20 s each, characterized by nonspecific motor activity, frontal desynchronization and theta rhythmic activity in the hippocampus. Consecutive epochs were taken to avoid selection bias. These episodes were compared to 42 small intervals of alertness intensification lasting 2 s at the beginning of exploratory behaviors, during which concomitant activation of the neck extensors, eye muscles and vibrissae was visually detected in the electromyograms. Only periods of clear signal artifact generated by head scratching or hitting the socket against the cage walls were suppressed. The modulation of the instantaneous frequency during exploratory behavior was then analyzed (see Supporting information). Moreover, the frequency spectrum was determined based on the finite Fourier transform. The power spectrum of these oscillations was determined according to the square of the Fourier transform (power spectrum, expressed as uV^2/Hz), based on Parseval's theorem for energy signals.

To predict the connection among structures, the partial directed coherence method was employed (28) for the theta band, here assumed to be 5-11 Hz. See Supporting information.

Electrode tracks and microlesions marking the final positions were identified in sections of formalin-fixed tissue cut at 40 µm and stained for the Nissl substance.

Statistical analysis

Mean data were compared by the Mann-Whitney U-test using the SPSS software (IBM, USA). Graphs were constructed with the Igor 5.04 tool (Wavemetrics, USA).

Results

We recorded a total of 7 animals for 62 h and selected the first 6 segments for each animal during which wakefulness lasted longer than 10 min. As mentioned above, we compared 42 epochs of wakefulness with unspecific motor activity, frontal desynchronization and theta rhythmic activity in the hippocampus, to 42 other 2-s intervals at the beginning of exploratory behavior, characterized by concomitant activation of the three electromyographic channels recorded. Oscillations in striatal LFP occur in the awake, behaving rat and are modulated by behavioral activity. Robust theta-band activity was evident in LFP recorded in the entire central processing unit during periods of spontaneous movement. During exploratory behavior, the power in the oscillatory signal was greatest for the theta band. Striatal theta activity was less prominent during grooming and during wakeful rest.

Overall, during exploration we observed a desynchronization in area 10 and in the rostral caudatoputamen, as well as theta activity at most of the striatal electrodes and in areas 6, 17, and CA3 (see Figures 2A and 3). Analysis of the instantaneous frequency revealed that striatal LFP signals oscillated in a narrow theta band. Figure 2B illustrates the variation in the instantaneous frequency for all recorded channels during the epoch shown in 2A. We recorded exploratory behavior between times 157 and 164 s and detected activity in the neck, vibrissae and eyes (highlighted with a red bar). Interestingly, striatal signals undergo fine modulation with brief periods of frequency convergence in the theta range, and this modulation was most prominent at the beginning and at the end of the exploratory behavior (marked with asterisks). This kind of modulation was not seen in A17 or CA3, and rarely seen in A6 and A10. Nevertheless, modulation was present in 92.5 ± 2.5% of all segments analyzed in the striatal channels; more specifically, 97.2 ± 2.3% in the CPur, 96.4 ± 2.1% in the CPudl, 95.3 ± 2.6% in the CPuv, 82.7 ± 2.2% in the CPum, and finally 91 ± 2.6% in the CPuc. Next we analyzed the power spectra in order to measure the relative contribution of each frequency to the recorded signals (see Figure 3). Overall, a clear predominance of theta activity was confirmed in all striatal areas. Comparing episodes of wakefulness to episodes of exploratory behavior, we observed an increase in theta spectra from 35 ± 3 to 40 ± 5 μV^2/Hz in the CPudl (P < 0.001), from 25 ± 2 to 59 ± 4 μV^2/Hz in the CPuv (P < 0.001), from 41 ± 5 to 61 ± 5 μV^2/Hz in the CPum (P < 0.001), and from 100 ± 7 to 170 ± 9 μV^2/Hz in the CPuc (P < 0.001).

Given that the theta rhythm was the most important component of striatal spectrograms during exploratory behavior, we next decided to investigate the coherence pattern in the theta range among the recorded structures during rest wakefulness and exploratory behavior. Figure 4 depicts this behavior, with A and B illustrating the contour

graphs of averaged coherence coefficients for all 40 segments studied, in wakefulness (A) and at the beginning of exploratory behaviors (B). Functionally distinct zones of the striatum exhibit coherent LFP oscillations during exploration. Additionally, the theta-band activity was highly synchronous within and across all recorded striatal regions, with coherence values of at least 0.7. A consistent increase in the partial directed coherence among all striatal channels and between CPur and A6 during attention periods was evident, a finding not repeated in any of the other pairs recorded. The coherence between CPur and A6, for example, increased from 0.9059 ± 0.0564 during wakefulness to 0.9626 ± 0.0224 ($P < 0.001$) during exploratory behavior. Similarly, the CPudl-CPuv pair showed increased coherence from 0.7799 ± 0.1318 to 0.8903 ± 0.0657 ($P < 0.001$); CPudl-CPum from 0.8041 ± 0.1173 to 0.8890 ± 0.0665 ($P < 0.001$); CPudl-CPuc from 0.7659 ± 0.1402 to 0.8228 ± 0.1061 ($P < 0.05$); CPuv-CPum from 0.7569 ± 0.1402 to 0.8746 ± 0.0751 ($P < 0.001$); CPuv-CPuc from 0.6607 ± 0.2032 to 0.7443 ± 0.1532 ($P < 0.5$), and finally CPum-CPuc from 0.9511 to 0.9494 ($P = 0.79$). Figure 4C and D show in tridimensional graphs the magnitude of the increase in coherence between the recorded pairs observed during increased attention. Taken together, these data support the notion that different anatomical regions of the rodent striatum interplay with high coherence in the theta band during increased attention related to environment exploration.

Discussion

In the present study, LFP recordings of distinct striatal structures in freely moving rats, concomitantly with prefrontal and motor cortical areas, revealed fine modulation of theta oscillations during exploratory behavior in all striatal channels, but not in the prefrontal or visual cortex. Moreover, the theta power spectrum increased throughout the 5 striatal channels recorded during exploration, in parallel with changes in behavioral patterns. Finally, partial directed coherence analyses revealed a closer connectivity between A6 and the rostral portion of the striatum, concomitant with increased activity among all other striatal channels. These results indicate that anatomically distinct parts of the rodent striatum
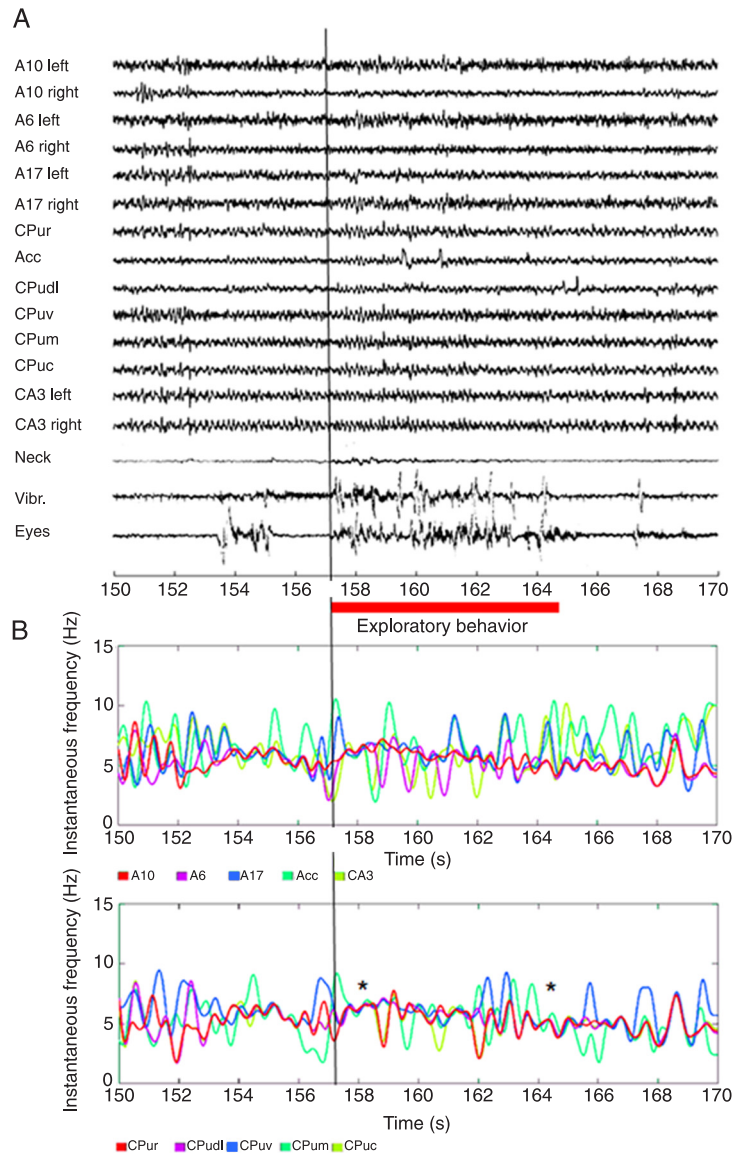

Figure 2. Striatal signals converge to theta frequencies during exploratory behavior. *A* shows an electroscillogram of a rat in the wake phase, exemplifying a typical exploratory behavior. Note the predominance of regular rhythmic activity between 6 and 10 Hz during alertness. At the time, the animal was awake and moving freely in the recording chamber. The theta rhythmic activity is more intense in the limbic and posterior cortical areas, but also predominates at almost all recorded striatal electrodes. Intense exploratory behavior was recorded between 157 and 164 s (highlighted with a red bar), characterized by movements of the neck, together with visual and olfactory exploration of the environment. *B* is a graphic representation of the variation in the instantaneous frequency across all recording channels. Note a convergence of the signals at the theta frequency range, in this case 6 Hz, concomitant with the beginning and end of muscle activity. This modulation was observed in all striatal channels (asterisks), as well as for A10 and A6. Interestingly, in A17 and CA3, a similar modulation occurred only at the beginning of the behavior, but not at the end.
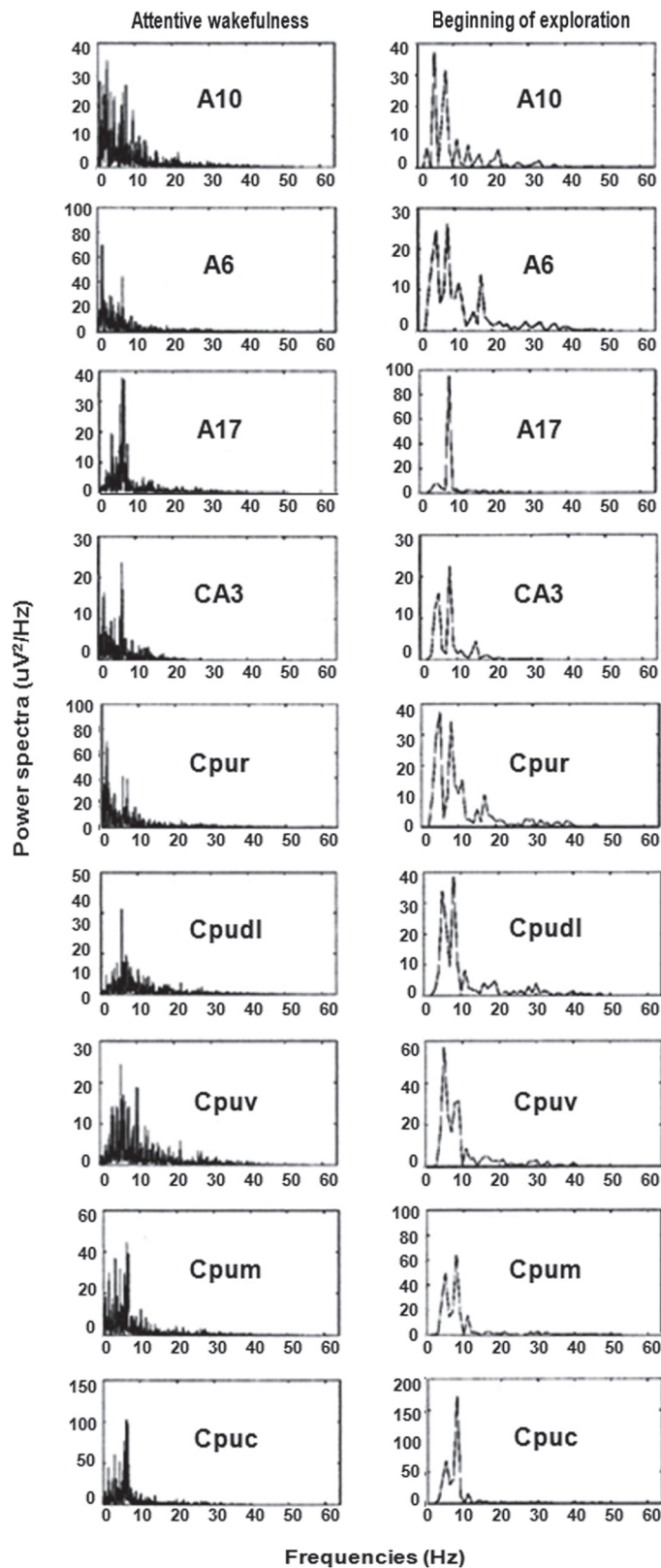
Figure 3. Increase in theta power spectra in all striatal areas during periods of increased attention. Attentive wakefulness was defined as predominance of desynchronization in the prefrontal cortex, theta rhythmic activity in the hippocampus, and general motor activity. Intensification of alertness during exploratory behavior was defined based on the initiation of concomitant muscle activity in the neck extensor muscles, eyes and vibrissae. We selected for analysis 2-s intervals at the beginning of exploratory behaviors and 20-s intervals of attentive wakefulness without exploratory movements. The power spectra of all recorded channels during periods of attentive wakefulness are represented on the left, and during exploratory behavior on the right. Robust theta band activity was evident in local field potentials recorded in the whole caudate putamen complex throughout periods of spontaneous movement during attentive wakefulness. At the beginning of exploratory behaviors, however, the power in the oscillatory signal was greatest at the 5-10 Hz band. Oscillatory activity was also present in the delta range (<5 Hz), beta range (10-30 Hz), and gamma range (30-50 Hz) as well. Theta activity was less prominent during grooming and during wakeful rest. For abbreviations, see legend to Figure 1.
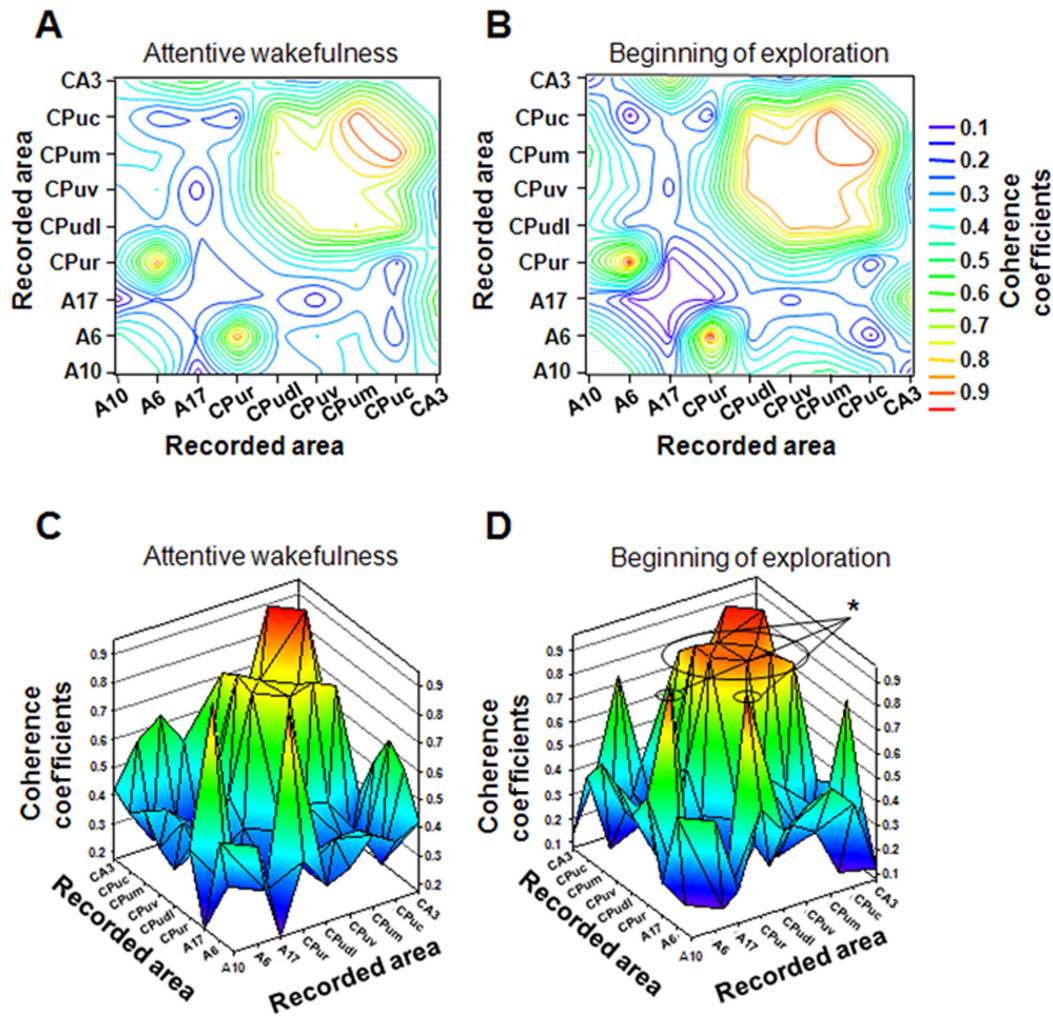
Figure 4. Increased coherence between the primary motor cortex and the head of the caudate nucleus, and among all caudate putamen (CPu) channels. *A* and *B*, Contour graphs showing the coherence coefficients (partial directed coherence in the theta band) among recorded areas during the whole segment lasting 20 s (*A*, left) and during the 2-s segment at the beginning of the exploratory behavior (*B*, right). Coefficient values are color-coded according to the legend on the right, where blue represents low coherence and red high coherence, without inference on information flow (see text). Note an increase in the coherence among all striatal channels and between A6 and the rostral caudate putamen (CPur) with increased attention. *C* and *D*, Three-dimensional representation of diagrams *A* and *B* to demonstrate the magnitude of this enhancement, evidenced by the red plateau and two red peaks in *D*. See text for absolute values and statistics. *$P < 0.001$, comparing the 2 initial seconds of the exploratory behavior with attentive wakefulness (Mann-Whitney U-test). For abbreviations, see legend to Figure 1.

actively participate in the organization of attention related to exploratory behavior, and oscillate with high coherence with the sensorimotor cortex in the theta band.

The timing of neuronal activity in the striatum is critical for motor and cognitive control. Our findings demonstrate that oscillatory activity is a prominent feature of locally generated field potential activity in the rat's striatum and show that, across a range of frequency bands, the power of the theta rhythm varies with spontaneous behavior. Our findings suggest that modulation of theta activity during

exploratory behavior may represent an important influence on corticostriatal loop function during attentive behavior. Theta rhythmicity in the striatum was most conspicuous during spontaneous running and environment exploration, and was weak during grooming and wakeful rest, when hippocampal theta is high. These characteristics held when the LFP recordings were in the medial, ventral, dorsolateral, head, and caudal portions of the striatum. The theta band oscillations recorded in these different regions were largely coherent. Although theta activity was concomitantly

measured in the hippocampus during exploration, this was not coherent with striatal LFP. It has been suggested that volume conduction can account for the rhythmic activity recorded in the striatum, due to electrotonic spread of the voltage signal from remote oscillators (29). Nevertheless, it has been shown that the striatal theta is not consistently correlated with the hippocampal theta during T-maze tasks (30). This demonstrates that the hippocampus is not responsible for the striatal rhythms. The low coherence in our experiments between the striatum and the hippocampus during environment exploration supports this notion.

Theta rhythmicity is thus a general characteristic of LFP activity in the striatum of rats actively exploring and moving in their environment. These results suggest that theta-band rhythmicity in the striatum does not depend exclusively on region-specific functions of particular striatal circuits. Rather, the LFP rhythms appear to be a shared feature of the temporal structuring of field activity in the striatum (31-33). The observed striatal LFP oscillations, as well as their marked coherence across all recording sites, may reflect the influence exerted by other sites such as neocortex, thalamus, and pallidum, or the activity of local striatal circuits operating in conjunction with these (31,34,35).

An important role attributed to the corticostriatal system is that of learning and memory. DeCoteau et al. (30) demonstrated that the coherence between striatal and hippocampal theta peaked during the decision period of tasks requiring navigational and cue-based associative learning, implying a key role of the striatum in cognitive processing. These investigators had previously demonstrated that there was no consistent relationship between the power of the theta band in the striatum and the primary characteristics of motor behavior, such as velocity or acceleration (32). This suggests that striatal theta activity may be linked to other behavioral state characteristics engaged during exploration of the environment. We propose here that the striatum may represent a relay station for distribution of attention to various neocortical areas. Our findings provide evidence that oscillatory activity in the striatum is systematically modulated by the behavioral context and especially according to the degree of attention; moreover, this activity seems to be coordinated across functionally different striatal regions.

In the present study, we conducted LFP recordings to demonstrate the predominance of synchronization in theta frequencies during attentive behavior in rodent striatum. The power spectra in theta increased during exploratory behavior, indicating a higher degree of activation during this time period. It is reasonable to assume that during environment exploration a higher degree of attention is being required. This modulation was observed in all striatal channels, highlighting the importance of the entire striatum during attention. Moreover, directed coherence analyses indicated strong connections during increased attention between area 6 and the rostral portion of the caudatoputamen complex, as well as among all striatal channels recorded. Our data conflict with results of previous studies that have demonstrated a tricompartmental striatal organization of associative, motor and limbic components, based on the connectivity patterns of these structures even in rats (6,8). The functional analysis of LFP during motor behavior in this study indicates concomitant activation of the whole striatum, as well as strong synchronization between the rostral striatum and the primary motor cortex during periods of increased attention. In an attempt to interpret these apparently divergent findings, we hypothesize that the three mental functions processed in the striatum - namely cognitive and associative aspects (integrated in the dorsolateral caudate nucleus), emotional status and reward (limbic ventral striatopallidal system) and motor planning (central putamen) - must all be concomitantly integrated during spontaneous behavior.

The data reported here serve to advance the current knowledge on basal ganglia function. We suggest that modulation of oscillatory activity in the striatum may be a key feature of neural processing related to the organization of attention and the integration of motor, cognitive, and limbic systems during voluntary behavior. Further experiments are needed to describe the electrophysiological alterations under pharmacological or surgical manipulation of this complex system.

Supporting information

Click here to view.

Acknowledgments

References

1. Ungerstedt U, Arbuthnott GW. Quantitative recording of rotational behavior in rats after 6-hydroxy-dopamine lesions of the nigrostriatal dopamine system. *Brain Res* 1970; 24: 485-493.
2. Evenden JL, Robbins TW. Effects of unilateral 6-hydroxydo-pamine lesions of the caudate-putamen on skilled forepaw use in the rat. *Behav Brain Res* 1984; 14: 61-68.
3. Marshall JF, Richardson JS, Teitelbaum P. Nigrostriatal bundle damage and the lateral hypothalamic syndrome. *J Comp Physiol Psychol* 1974; 87: 808-830.

4. Whishaw IQ, O'Connor WT, Dunnett SB. The contributions of motor cortex, nigrostriatal dopamine and caudate-putamen to skilled forelimb use in the rat. *Brain* 1986; 109 (Part 5): 805-843.

5. Ljungberg T, Ungerstedt U. Sensory inattention produced by 6-hydroxydopamine-induced degeneration of ascending dopamine neurons in the brain. *Exp Neurol* 1976; 53: 585-600.

6. Nauta WJ, Domesick VB. Afferent and efferent relationships of the basal ganglia. *Ciba Found Symp* 1984; 107: 3-29.

7. Nauta WJ. Limbic innervation of the striatum. *Adv Neurol* 1982; 35: 41-47.

8. Alexander GE, Crutcher MD, DeLong MR. Basal ganglia-thalamocortical circuits: parallel substrates for motor, oculo-motor, "prefrontal" and "limbic" functions. *Prog Brain Res* 1990; 85: 119-146.

9. Alheid GF, Heimer L. Theories of basal forebrain organiza-tion and the "emotional motor system". *Prog Brain Res* 1996; 107: 461-484.

10. Heimer L, Alheid GF. Piecing together the puzzle of basal forebrain anatomy. *Adv Exp Med Biol* 1991; 295: 1-42.

11. DeLong MR, Alexander GE, Georgopoulos AP, Crutcher MD, Mitchell SJ, Richardson RT. Role of basal ganglia in limb movements. *Hum Neurobiol* 1984; 2: 235-244.

12. Kunzle H. Projections from the primary somatosensory cor-tex to basal ganglia and thalamus in the monkey. *Exp Brain Res* 1977; 30: 481-492.

13. Goldman PS, Nauta WJ. An intricately patterned prefronto-caudate projection in the rhesus monkey. *J Comp Neurol* 1977; 72: 369-386.

14. Riedel A, Hartig W, Seeger G, Gartner U, Brauer K, Arendt T. Principles of rat subcortical forebrain organization: a study using histological techniques and multiple fluorescence labeling. *J Chem Neuroanat* 2002; 23: 75-104.

15. Benchenane K, Peyrache A, Khamassi M, Tierney PL, Gio-anni Y, Battaglia FP, et al. Coherent theta oscillations and reorganization of spike timing in the hippocampal-prefrontal network upon learning. *Neuron* 2010; 66: 921-936.

16. Kahana MJ, Seelig D, Madsen JR. Theta returns. *Curr Opin Neurobiol* 2001; 11: 739-744.

17. Buzsaki G, Draguhn A. Neuronal oscillations in cortical net-works. *Science* 2004; 304: 1926-1929.

18. Linkenkaer-Hansen K, Nikulin VV, Palva S, Ilmoniemi RJ, Palva JM. Prestimulus oscillations enhance psychophysi-cal performance in humans. *J Neurosci* 2004; 24: 10186-10190.

19. Womelsdorf T, Fries P, Mitra PP, Desimone R. Gamma-band synchronization in visual cortex predicts speed of change detection. *Nature* 2006; 439: 733-736.

20. Buzsaki G, Chrobak JJ. Synaptic plasticity and self-organization in the hippocampus. *Nat Neurosci* 2005; 8: 1418-1420.

21. Hasselmo ME. What is the function of hippocampal theta rhythm? - Linking behavioral data to phasic properties of field potential and unit recording data. *Hippocampus* 2005; 15: 936-949.

22. Vertes RP, Hoover WB, Viana Di Prisco G. Theta rhythm of the hippocampus: subcortical control and functional signifi-cance. *Behav Cogn Neurosci Rev* 2004; 3: 173-200.

23. Berke JD, Okatan M, Skurski J, Eichenbaum HB. Oscillatory entrainment of striatal neurons in freely moving rats. *Neuron* 2004; 43: 883-896.

24. van der Meer MA, Redish AD. Theta phase precession in rat ventral striatum links place and reward information. *J Neurosci* 2011; 31: 2843-2854.

25. Andersen ML, Valle AC, Timo-Iaria C, Tufik S. *Implantação de elétrodos para o estudo eletrofisiológico do ciclo vigília-sono do rato*. São Paulo: Ed. UNIFESP; 2001.

26. Paxinos G, Watson C. *The rat brain in stereotaxic coordi-nates*. 4th edn. New York: Elsevier; 2004.

27. Zilles KJ. *The cortex of the rat: a stereotaxic atlas*. Berlin, New York: Springer-Verlag; 1985.

28. Sameshima K, Baccala LA. Using partial directed coherence to describe neuronal ensemble interactions. *J Neurosci Methods* 1999; 94: 93-103.

29. Sirota A, Montgomery S, Fujisawa S, Isomura Y, Zugaro M, Buzsaki G. Entrainment of neocortical neurons and gamma oscillations by the hippocampal theta rhythm. *Neuron* 2008; 60: 683-697.

30. DeCoteau WE, Thorn C, Gibson DJ, Courtemanche R, Mitra P, Kubota Y, et al. Learning-related coordination of striatal and hippocampal theta rhythms during acquisition of a procedural maze task. *Proc Natl Acad Sci U S A* 2007; 104: 5644-5649.

31. Courtemanche R, Fujii N, Graybiel AM. Synchronous, focally modulated beta-band oscillations characterize local field potential activity in the striatum of awake behaving monkeys. *J Neurosci* 2003; 23: 11741-11752.

32. DeCoteau WE, Thorn C, Gibson DJ, Courtemanche R, Mitra P, Kubota Y, et al. Oscillations of local field potentials in the rat dorsal striatum during spontaneous and instructed behaviors. *J Neurophysiol* 2007; 97: 3800-3805.

33. Magill PJ, Pogosyan A, Sharott A, Csicsvari J, Bolam JP, Brown P. Changes in functional connectivity within the rat striatopallidal axis during global brain activation *in vivo*. *J Neurosci* 2006; 26: 6318-6329.

34. Aldridge JW, Gilman S. The temporal structure of spike trains in the primate basal ganglia: afferent regulation of bursting demonstrated with precentral cerebral cortical abla-tion. *Brain Res* 1991; 543: 123-138.

35. Lebedev MA, Nelson RJ. Rhythmically firing neostriatal neurons in monkey: activity patterns during reaction-time hand movements. *J Neurophysiol* 1999; 82: 1832-1842.