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# MODALITY DISTRIBUTION OF SENSORY NEURONS IN THE FELINE CAUDATE NUCLEUS AND THE SUBSTANTIA NIGRA

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Despite extensive analysis of the motor functions of the basal ganglia and the fact that multisensory information processing appears critical for the execution of their behavioral action, little is known concerning the sensory functions of the caudate nucleus (CN) and the substantia nigra (SN). In the present study, we set out to describe the sensory modality distribution and to determine the proportions of multisensory units within the CN and the SN. The separate single sensory modality tests demonstrated that a majority of the neurons responded to only one modality, so that they seemed to be unimodal. In contrast with these findings, a large proportion of these neurons exhibited significant multisensory cross-modal interactions. Thus, these neurons should also be classified as multisensory. Our results suggest that a surprisingly high proportion of sensory neurons in the basal ganglia are multisensory, and demonstrate that an analysis without a consideration of multisensory cross-modal interactions may strongly underrepresent the number of multisensory units. We conclude that a majority of the sensory neurons in the CN and SN process multisensory information and only a minority of these units are clearly unimodal.

*Keywords:* Visual – auditory – somatosensory – multisensory integration – basal ganglia

## INTRODUCTION

The basal ganglia are widely regarded as structures involved in sensorimotor coordination [1, 11, 21]. Despite the fact that multisensory information processing appears critical for the execution of the behavioral role of the caudate nucleus (CN) and the substantia nigra (SN) [3], little is known concerning the sensory background of their functions. The results accumulated to date have provided evidence of the existence of neurons sensitive to visual, auditory, and somatosensory modalities, and multisensory neurons have been found in the CN and the SN [4, 7–9, 12, 15–20, 24].

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These results indicated that a majority of the sensory neurons in the CN and SN are unimodal, in the sense that they reacted to a statistically significant extent only to visual or auditory or somatosensory stimulation, and merely a minority of the units were multisensory, i.e. they responded to more than one sensory modality when these were presented separately [4, 12, 17, 19].

Similarly as for the superior colliculus (SC) [10, 13, 14, 23, 26, 28, 29] and the cortical regions along the anterior ectosylvian sulcus (AES cortex) [2, 27], brain structures that provide the multisensory information toward the basal ganglia [5, 6], cross-modal response enhancement and cross-modal response depression were also found in the CN and the SN [4, 18, 30]. In order to determine the correct proportions of the multisensory neurons and the modality distribution of the sensory neurons in the SN and the CN, we recorded and analyzed the responses of the single neurons to visual, auditory, somatosensory and also multisensory stimulation in anesthetized, paralyzed cats.

## MATERIALS AND METHODS

### *Animal preparation and surgery*

This study was performed on 7 adult cats of either sex, weighing between 2.8 and 3.3 kg. All procedures were carried out in such a way as to minimize the number and the suffering of the animals, and followed the European Communities Council Directive of 24 November 1986 (S6 609 EEC) and the National Institute of Health guidelines for the care and use of animals for experimental procedures. The experimental protocol was accepted by the Ethical Committee for Animal Research of Albert Szent-Györgyi Medical and Pharmaceutical Center at the University of Szeged. The cats were initially anesthetized with ketamine hydrochloride (30 mg/kg i.m.). The trachea and the femoral vein were cannulated and the animals were placed in a stereotaxic headholder. The head of each animal was fixed to a vertical metal bar with the aid of acrylate and the ear-bars were removed. Wound edges were treated generously with procaine hydrochloride (1%). The anesthesia was continued with halothane (1.6–2.4% during surgery and 0.8–1.0% during recordings). The depth of anesthesia was monitored by continuous reading of the end-tidal halothane values and by repeated checks of the electroencephalogram (EEG) and electrocardiogram. There was continuous high-amplitude, low-frequency EEG activity. We checked repeatedly that any noxious stimulation or a forceful pressing of the forepaws should not induce EEG desynchronization. The minimal alveolar anesthetic concentrations calculated from the end-tidal halothane readings were always in the range given by Villeneuve and Casanova [25]. The animals were immobilized with gallamine triethiodide (Flaxedyl, 20 mg/kg i.v.). A liquid containing gallamine (8 mg/kg/h), glucose (10 mg/kg/h) and dextran (50 mg/kg/h) in Ringer solution was infused at a rate of 3 ml/h. The end-tidal $CO_2$ level and the rectal temperature were monitored continuously and kept approximately constant, at 3.8–4.2% and 37–38 °C, respectively.

The skull was opened with a dental drill to allow a vertical approach to the appropriate brain structures. The dura was removed and the cortical surface was covered with a 4% solution of 38 °C agar dissolved in Ringer solution. The eye contralateral to the cortical recording was treated with phenylephrine (10%) and atropine (0.1%), and was equipped with a +2 diopter contact lens. The ipsilateral eye was covered during visual stimulation. A subcutaneous injection of 0.2 ml 0.1% atropine was administered preoperatively.

## *Recording and stimulation*

Electrophysiological recordings on single-units were carried out extracellularly via tungsten microelectrodes (AM System Inc. USA, 2–4 MOhm). Vertical penetrations were performed between the Horsley-Clarke co-ordinates anterior: 12–16, lateral: 4–6.5 in the stereotaxic depths between 12 and 19, and anterior: 3–6, lateral: 4–6 in the stereotaxic depths between 4 and 7, to record CN and SN single-units, respectively, according to "The stereotaxic atlas of the cat brain" by Snider and Niemer [22]. At the end of the experiments, the animals were deeply anesthetized with sodium pentobarbital (200 mg/kg i.v.) and transcardially perfused with 4% paraformaldehyde solution. The brains were removed, cut in coronal sections of 50 μm and stained either with neutral red in the CN, or with Nissl staining in the SN. Recording sites were localized via the marks of electrode penetrations (Fig. 1).

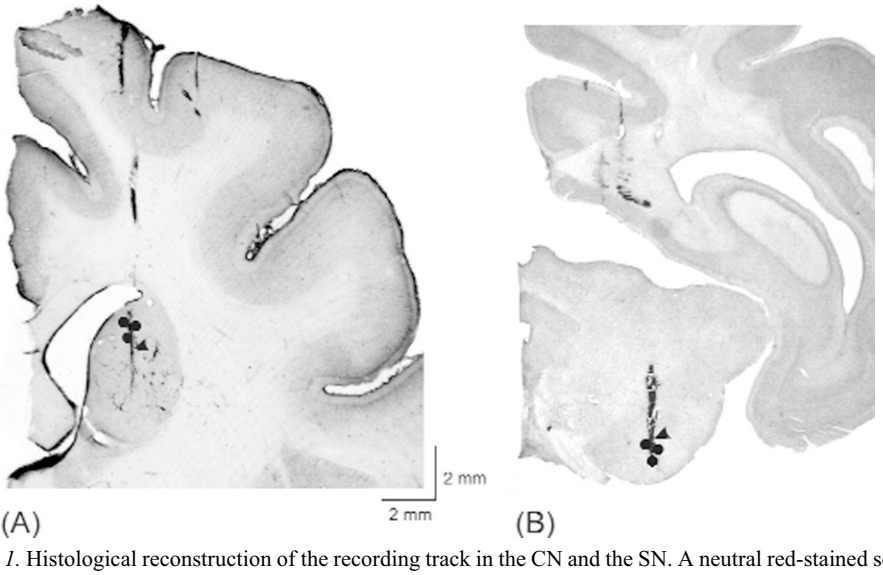



*Fig. 1.* Histological reconstruction of the recording track in the CN and the SN. A neutral red-stained section from the CN (A) and a Nissl-stained section from the SN (B) within the position of the recording electrode is marked by the black arrowhead. Black dots represent the location of some recorded neurons. Bars in the right bottom corner of the A part of the figure provide size calibration and orientation in the dorso-ventral and medio-lateral aspect

For visual stimulation, light spots 1–10° in diameter (depending on the stimulus size preference of each unit) were generated by a projector device equipped with an adjustable slit-lamp diaphragm. The mean luminance of the stimulus was 23 cd/m$^2$. The high-contrast (70%) visual stimuli were moved through the area centralis with a computer-controlled moving mirror system and were projected across the tangent screen (52 cm in front of the animal) in the optimal moving direction and at an optimal velocity (30–120°/s) for each unit. The duration of stimulus movement was 1000 ms. The white noise auditory stimuli were produced by a loudspeaker positioned on the tangent screen 52 cm in front of the animal to the back reflection of the area centralis. The sound intensity near the speaker was constant at 60 dB. The duration of the auditory stimulation was 1000 ms. Somatosensory stimulation was delivered with the motion of a computer-controlled pen driver, whose tip was attached to nylon fibers. The surface area of the stimulator was 1 cm$^2$. The hair was shaved at the stimulation site. The stimulator was rotated and provided a constant light mechanical stimulation (pressing) on a constant 1 cm$^2$ surface of the contralateral trunk of the animal. The duration of a somatosensory stimulation was also 1000 ms. The computer-controlled stimuli were presented in a pseudo-random order, either separately (visual or auditory or somatosensory) or simultaneously in bimodal (visual-auditory, visual-somatosensory or auditory-somatosensory) or trimodal (visual-auditory-somatosensory) combinations. Whenever a single unit was found that was visual or auditory or somatosensory-sensitive, at least 10 trials were run in each condition. The interstimulus interval was consistently 1000 ms.

Individual action potentials were distinguished with the help of a spike-separator system (SPS-8701, Australia). The number and temporal distribution of the action potentials recorded during visual, auditory, somatosensory, bimodal or trimodal stimulations were stored as peristimulus time histograms (PSTHs) and analyzed off-line by computer. Both the prestimulus time (during which we measured the spontaneous activity of the neurons) and the peristimulus time (during which we measured the neuronal responses to different sensory and multisensory stimulations) were 1000 ms.

## *Data analysis*

The net firing rate was calculated as the difference between the firing rates during the prestimulus (1000 ms) and the peristimulus (1000 ms) intervals. When we analyzed the neuronal responses to separate visual, auditory or somatosensory stimulation and multisensory stimulus combinations, we defined the net firing rate as the response when a paired *t*-test indicated a significant ($p < 0.05$) difference between the prestimulus and the peristimulus firing rates.

A cross-modal multisensory interaction was considered to exist when the difference between the net firing rate of the most effective single modality and the bimodal or trimodal peristimulus firing rate proved to be significant on analysis of variance (ANOVA, $p < 0.05$) [10, 13].

## RESULTS

We investigated the responses of 77 CN and 75 SN pars reticulata excitatory responsive single neurons to separate visual, auditory or somatosensory stimulus presentations and after multisensory stimulation. The background activity of the SN pars reticularis neurons (N = 75; mean = 25.3 sp/sec, SD: ± 5.9 sp/sec, range: 8–58 sp/sec) was significantly higher (*t*-test for independent samples, $p < 0.01$) than that of the CN neurons (N = 77; mean = 9.0 sp/sec, SD: ± 7.1 sp/sec, range: 1–31 sp/sec).

### *A majority of the CN and SN units in the separate single modality tests seem to be unimodal*

The classification based only on the significant responses of the CN and SN neurons to the separate sensory modalities demonstrated that a majority of the CN (50/77, 65%) and SN (38/75, 51%) neurons seemed to be unimodal, reacting to a statistically significant extent to only one of the investigated modalities, and only a smaller proportion of the units exhibited a multisensory character (27/77, 35% in the CN and 37/75, 49% in the SN), reacting to a statistically significant extent to two or three different sensory modalities (Tables 1A and 2A).

*Table 1*
Modality distribution of sensory neurons in the caudate nucleus (CN)

| Modality | A | | B | |
|---|---|---|---|---|
| *Unimodal* | 50 | (65%) | 25 | (32%) |
| Visual | 22 | (29%) | 10 | (13%) |
| Auditory | 8 | (10%) | 4 | (5%) |
| Somatosensory | 20 | (26%) | 11 | (14%) |
| *Multisensory* | 27 | (35%) | 52 | (68%) |
| Visual-auditory | 7 | (9%) | 9 | (12%) |
| Visual-somatosensory | 9 | (12%) | 14 | (18%) |
| Auditory-somatosensory | 3 | (4%) | 10 | (13%) |
| Trimodal | 8 | (10%) | 19 | (25%) |
| *Altogether* | 77 | (100%) | 77 | (100%) |

A: Modality distribution of CN neurons in separate sensory modality tests without multisensory stimulus combinations.

B: Modality distribution of CN neurons when multisensory combinations and multisensory interactions were also analyzed. Note the much higher number of multisensory units when multisensory integration was also analyzed. Thus, the separate sensory modality test without the analysis of multisensory responses may strongly underrepresent the number of multisensory units in the CN

*Table 2*
Modality distribution of sensory neurons in the substantia nigra (SN)

| Modality | A | | B | |
|---|---|---|---|---|
| *Unimodal* | 38 | (51%) | 15 | (20%) |
| Visual | 17 | (23%) | 5 | (7%) |
| Auditory | 3 | (4%) | 0 | (0%) |
| Somatosensory | 18 | (24%) | 10 | (13%) |
| *Multisensory* | 37 | (49%) | 60 | (80%) |
| Visual-auditory | 5 | (7%) | 6 | (8%) |
| Visual-somatosensory | 16 | (21%) | 19 | (25%) |
| Auditory-somatosensory | 5 | (7%) | 5 | (7%) |
| Trimodal | 11 | (14%) | 30 | (40%) |
| *Altogether* | 75 | (100%) | 75 | (100%) |

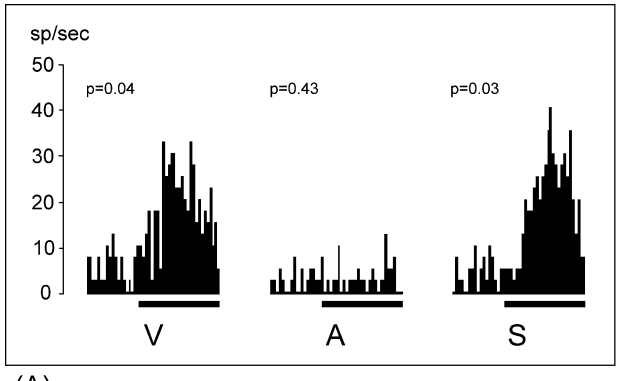
A: Modality distribution of SN neurons in separate sensory modality tests without multisensory stimulus combinations.

B: Modality distribution of the SN neurons when multisensory combinations and multisensory interactions were also analyzed. Note the much higher number of multisensory units when multisensory integration was also tested. Thus, the separate sensory modality test without the analysis of multisensory responses may strongly underestimate the number of multisensory units in the SN

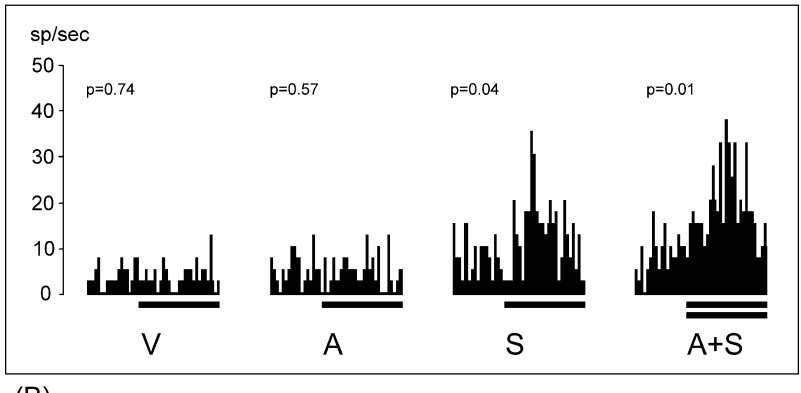
## *Is unimodal clearly unimodal? Or is it after all multisensory in some cases?*

In order to analyze the multisensory information-processing abilities of the same 77 CN and 75 SN neurons, we also recorded the neuronal responses of these units to multisensory stimulus combinations. We found that 36 of the 77 investigated CN neurons (47%) and 41 of the 75 SN neurons (55%) exhibited significant multisensory cross-modal interactions. Surprisingly, only 11 of these 36 CN and 18 of these 41 SN integrative cells had been defined as multisensory in the separate single modality tests, i.e. these units responded to a statistically significant extent to at least two different sensory modalities presented alone (Figs 2A, 3A). In contrast, a larger proportion of the integrative CN and SN units responded in a separate modality test to only one sensory modality, and thus these units were classified as unimodal on the basis of the results of the separate single modality tests. Twenty-five of the 36 integrative CN cells (12 visual, 3 auditory and 10 somatosensory) and 23 of the 41 integrative SN units (12 visual, 3 auditory and 8 somatosensory) with a significant cross-modal interaction had responded to a statistically significant extent only to individual auditory or visual or somatosensory stimulation, but the originally ineffective modality or modalities were able to induce multisensory interactions (Figs 2B, 3B). Ten of the 25 CN units that were classified earlier as unimodal displayed a significant multisensory interaction with only one ineffective modality presented together

with the effective stimulus, i.e. these units seemed to be bimodal. The other 15 units must be classified as trimodal, because 10 of these cells exhibited interactions with both ineffective modalities or exhibited facilitatory interactions only on trimodal stimulus presentation. Similarly, 8 of the 23 SN units classified earlier as unimodal demonstrated an interaction with only one ineffective modality, while the other 15 neurons were trimodal in the sense that 11 cells revealed interactions with both inef-




(A)




(B)

*Fig. 2.* Multisensory responses of two CN neurons. (A): Responses of a multisensory CN neuron that responded significantly to both visual and somatosensory stimulation in the separate single modality tests. The left PSTH demonstrates the neuronal response to visual (V), the middle one to auditory (A) and the right one to somatosensory (S) stimulation. (B): Responses of a multisensory CN neuron that responded significantly to only somatosensory stimulation in the separate single modality tests, but the ineffective auditory stimulus presented simultaneously with the somatosensory stimulus induced a significant multisensory response enhancement. The left PSTH demonstrates the neuronal response to visual (V), the second one to auditory (A), the third one to somatosensory (S) and the right one to combined auditory-somatosensory (A+S) stimulation. The p value above each PSTH denotes the significance level of a response. Each PSTH shows the single-unit activities before and during (indicated by thick black lines) stimulation. The thick black lines indicate stimulation intervals of 1000 ms. The calibration denotes the firing rates (sp/s)

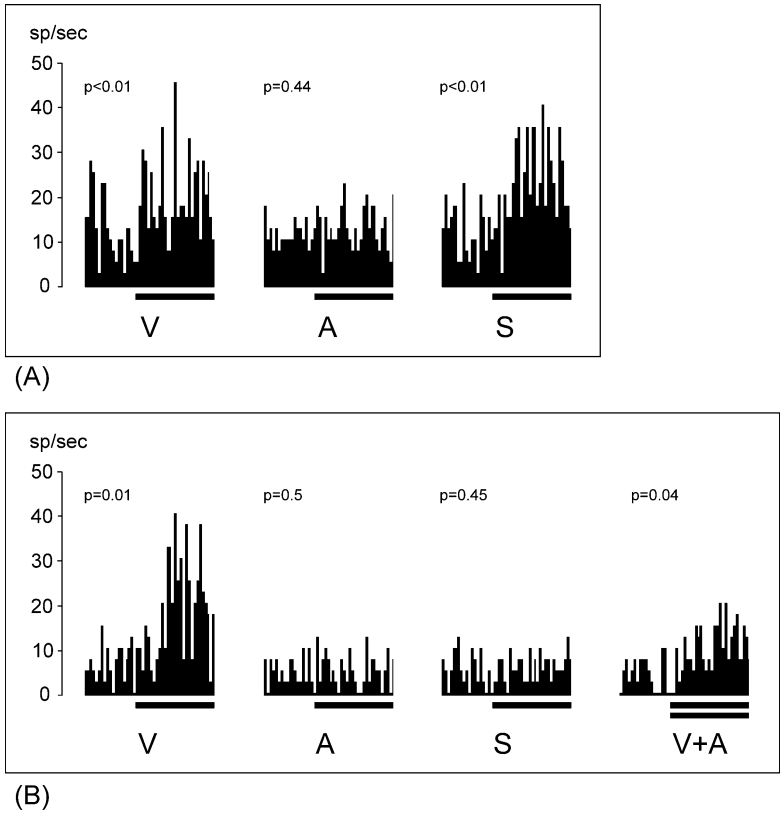



*Fig. 3.* Multisensory responses of two SN neurons. (A): Responses of a multisensory SN neuron that responded significantly to both visual and somatosensory stimulation in the separate single modality tests. The left PSTH demonstrates the neuronal response to visual (V), the middle one to auditory (A) and the right one to somatosensory (S) stimulation. (B): Responses of a multisensory SN neuron that responded significantly to only visual stimulation in the separate single modality tests, but the ineffective auditory stimulus presented simultaneously with the visual stimulus induced a significant multisensory response depression. The left PSTH demonstrates the neuronal response to visual (V), the second one to auditory (A), the third one to somatosensory (S) and the right one to combined visual-auditory (V+A) stimulation. The conventions are the same as in Figure 2

fective modalities and 4 units displayed facilitatory interactions only on trimodal stimulus presentation. Thus, despite the consistent results of the neuronal responses to separate sensory stimulations, these 25 CN and 23 SN units seem to be multisensory. Thus, a majority of the investigated CN (52/77, 68%) and SN (60/75, 80%) units proved to be of a multisensory character, and only a smaller proportion of them (25/77, 32% in the CN, and 15/75, 20% in the SN) were classified as absolutely unimodal (Tables 1B and 2B). We compared the modality distribution in the CN and the SN we found that there's a significant difference between the modality distributions in the two structures (Pearson Chi-square test: $\chi^2 = 16.95$; $df = 6$; $p < 0.01$).

## DISCUSSION

Our results furnish new data concerning the multimodal representation of the environment in the basal ganglia of the mammalian brain. We recorded the neuronal responses in the CN and SN of anaesthetized, paralyzed cats to visual, auditory or somatosensory stimulation alone and also to their combinations, i.e. multisensory stimuli. Our results suggest that the large majority of the sensory neurons in both structures could process multisensory information, which suggests the existence of strong multisensory pathways conveying sensory information to the basal ganglia.

We investigated the modality distribution of the CN and SN sensory units in the first step in the single modality tests without multisensory stimulation. The statistical analysis of the neuronal responses to separately presented visual or auditory or somatosensory stimulation suggested that the majority of the sensory units in both investigated structures seemed to be unimodal, in the sense that they only responded to one sensory modality tested to a statistically significant extent. The majority of the neurons in the CN and the SN responded to visual or somatosensory stimulation and only a smaller proportion responded to auditory stimulation. Earlier studies of our group suggested that the sensory neurons in the CN and the SN can be involved in the sensory feedback of motor actions connected to self-movements [15–18]. In this aspect the visual and somatosensory information seem to be more important for these neurons than the auditory one. These results indicate that the majority of the single sensory neurons process only one sensory modality information, while only a smaller proportion of the neurons have the ability to process complex multisensory stimuli. Similar results were found in the AES cortex and the SC where the large majority of the units were also responsive to only one sensory modality in the separate modality tests [2, 13, 14]. Further investigation of the neuronal responses in the AES cortex and the SC to multisensory stimulus complexes and the analysis of multisensory integration in these structures demonstrated that a significant proportion of these units classified earlier unimodal exhibited significant and strong multisensory cross-modal response enhancement or response depression [2, 14]. Any single neuron that exhibited a significant cross-modal response enhancement or depression has to be classified as multisensory despite that during the single modality tests they responded to one sensory modality stimulation.

In order to update the modality distribution and give the accurate proportion of unimodal and multisensory units in the CN and the SN we analyzed in the next step the responses of the same 77 CN and 75 SN pars reticulata neurons to multisensory stimulus complexes (visual-auditory, visual-somatosensory, auditory-somatosensory and trimodal). We found that a significant proportion of in the single modality tests unimodal classified neurons elicited multisensory cross-modal interactions. Thus, the ineffective modality or modalities combined with the effective modality could induce either multisensory response enhancement or in some cases multisensory response depression. Despite of the unimodal character of these units in the single modality tests the multisensory stimuli mean more these units than the unimodal components presented alone. We classified these integrative units in the updated modality distri-

bution of the sensory CN and SN neurons as multisensory. Thus, the analysis of the neuronal responsivity to separate visual, auditory and somatosensory stimulation without any combination of the modalities may have strongly underrepresented the number of multisensory units in the basal ganglia [4, 12, 17, 19].

These results demonstrated that in our sample, a large majority of the sensory CN and SN neurones were multisensory. Similarly, high number of multisensory units (> 50%) were found in the SC [13, 14, 23, 28], but the number of multisensory units described in the anterior ectosylvian area (AEV) (about 20%) is much lower [2, 27]. We found that among the multisensory neurons in the CN and the SN the majority of the cells responded to trimodal or visual-somatosensory bimodal stimulation, which gives further evidence for the importance of visual and somatosensory information processing in the basal ganglia.

We found a difference between the modality distributions and the number of multisensory neurons between the CN and the SN. The SN contains significantly more multisensory units than the CN. The explanation for this can be either the small number of the analyzed neurons in the present study or more likely that the SN represents a higher order structure than the CN involved in multisensory information processing and multisensory convergence.

Our results gave evidence that the large majority of the CN and SN units have the ability to process and integrate multisensory information and only minority of the units are clearly unimodal. The functional importance of multisensory information processing may be the more accurate detection of the relevant sensory events in the complex multisensory enviroment [13, 14, 23]. The multisensory CN and the SN neurons may play a prominent role in the senso-motor integration. These neurons may record the changes in the multisensory environment during self-movement of the animal and thus the basal ganglia may participate in the adjustment of motor behavior in response to environmental challenges.

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