2013


Transmission of information in the corticospinal (CS) route constitutes the fundamental infrastructure for voluntary actions. The anatomy of this pathway has been studied extensively, but there is little direct evidence regarding its functional organization. Here we explored the areal specificity of CS connections by studying two related questions: the functional significance of the parallel, motor, and premotor CS pathways; and the way in which finger-related motor commands are handled by this pathway. We addressed these questions by recording from primary motor (M1) and premotor cortical sites in primates (Macaca fascicularis) performing a motor task, while measuring the evoked intraspinal unit response to single pulse cortical stimulation. Stimulation in M1 evoked spinal neuronal responses more frequently than stimulation in premotor cortex. The number of muscles excited by M1 stimulation was higher than the number excited by premotor stimulation. Within subregions of M1 finger-related sites were sparsely connected with intermediate zone interneurons and tended to affect the ventrally located motoneurons directly. These results suggest that, despite the parallel anatomical organization, the flow of motor commands is predominantly relayed via M1 to downstream elements. The functional impact of premotor cortex is weak, possibly due to inhibitory systems that can shape the flow of information in the CS pathway. Finally, the difference in spinal processing of finger versus wrist-related motor commands points to a different motor control strategy of finger versus wrist movements.

2012


The basal ganglia (BG) have been hypothesized to implement a reinforcement learning algorithm. However, it is not clear how information is processed along this network, thus enabling it to perform its functional role. Here we present three different encoding schemes of visual cues associated with rewarding, neutral, and aversive outcomes by BG neuronal populations. We studied the response profile and dynamical behavior of two populations of projection neurons [striatal medium spiny neurons (MSNs), and neurons in the external segment of the globus pallidus (GPe)], and one neuromodulator group [striatal tonically active neurons (TANs)] from behaving monkeys. MSNs and GPe neurons displayed sustained average activity to cue presentation. The population average response of MSNs was composed of three distinct response groups that were temporally differentiated and fired in serial episodes along the trial. In
the GPe, the average sustained response was composed of two response groups that were primarily differentiated by their immediate change in firing rate direction. However, unlike MSNs, neurons in both GPe response groups displayed prolonged and temporally overlapping persistent activity. The putamen TANs stereotyped response was characterized by a single transient response group. Finally, the MSN and GPe response groups reorganized at the outcome epoch, as different task events were reflected in different response groups. Our results strengthen the functional separation between BG neuromodulators and main axis neurons. Furthermore, they reveal dynamically changing cell assemblies in the striatal network of behaving primates. Finally, they support the functional convergence of the MSN response groups onto GPe cells.

2011


Controlling motor actions requires online adjustments of time-varying parameters. Although numerous studies have attempted to identify the parameters coded in different motor sites, the relationships between the temporal profile of neuronal responses and the dynamics of motor behavior remain poorly understood in particular because motor parameters such as force and movement direction often change over time. We studied time-dependent coding of cortical and spinal neurons in primates performing an isometric wrist task with an active hold period, which made it possible to segregate motor behavior into its phasic and sustained components. Here, we show that cortical neurons transiently code motor-related parameters when actively acquiring a goal, whereas spinal interneurons provide persistent information regarding maintained torque level and posture. Moreover, motor cortical neurons differed substantially from spinal neurons with regard to the evolvement of parameter-specific coding over the course of a trial. These results suggest that the motor cortex and spinal cord use different control policies: Cortical neurons produce transient motor commands governing ensuing actions, whereas spinal neurons exhibit sustained coding of ongoing motor states. Hence, motor structures downstream to M1 need to integrate cortical commands to produce state-dependent spinal firing.

2010


Current anatomical models of the cortico-basal ganglia (BG) network predict reciprocal discharge patterns between the external and internal segments of the globus pallidus (GPe and GPi, respectively), as well as cortical driving of BG activity. However, physiological studies revealing similarity in the transient responses of GPe and GPi neurons cast doubts on these predictions. Here, we studied the discharge properties of GPe, GPi, and primary motor cortex neurons of two monkeys in two distinct states: when eyes are open versus when they are closed. Both pallidal populations exhibited decreased discharge rates in the "eye closed" state accompanied by elevated values of the coefficient of variation (CV) of their interspike interval (ISI) distributions. The pallidal modulations in discharge patterns were partially attributable to larger fractions of longer ISIs in the "eye closed" state. In addition, the pallidal discharge modulations were
gradual, starting prior to closing of the eyes. Cortical neurons, as opposed to pallidal neurons, increased their discharge rates steeply on closure of the eyes. Surprisingly, the cortical rate modulations occurred after pallidal modulations. However, as in the pallidum, the CV values of cortical ISI distributions increased in the "eye closed" state, indicating a more bursty discharge pattern in that state. Thus changes in GPe and GPi discharge properties were positively correlated, suggesting that the subthalamic nucleus and/or the striatum constitute the main common driving force for both pallidal segments. Furthermore, the early, unexpected changes in the pallidum are better explained by a subcortical rather than a cortical loop through the BG.


Visuomotor transformation is a fundamental process in executing voluntary actions. The final steps of this transformation are presumed to take place in the corticospinal (CS) system, yet the way in which the motor cortex (MC) interacts with spinal circuitry during this process is unclear. We studied neural correlates of visuomotor transformation in the MC and cervical spinal cord while monkeys performed an isometric wrist task. We recorded 2 measures of population activity: local field potential (LFP), reflecting local synaptic inputs and multi-unit activity (MUA), reflecting spiking activity emitted by nearby neurons. We found robust cortical and spinal responses locked to visual and motor events. In motor cortex, LFP responses were predominantly visually related; MUA responses were mostly motor related. Spinal LFP responses were generally weak, yet spinal MUAs showed visual and motor responses with distinctive patterns. For both structures, amplitudes of visual responses were positively correlated with amplitudes of motor responses and negatively correlated with reaction times. The temporal relations of cortical and spinal responses shifted from weak coactivation before movement to increased coupling following torque onset, with cortical leading spinal activity. Thus, ongoing CS interactions may exist at early stages of movement preparation. These interactions are dynamic and may shape the executed motor action.


Corticospinal interactions are considered to play a key role in executing voluntary movements. Nonetheless several different studies have shown directly and indirectly that these interactions take place long before movement starts, when preparation for forthcoming movements dominates. When motor-related parameters are continuously processed in several premotor cortical sites, segmental circuitry is directly exposed to this processing via descending pathways which originate from these sites in parallel to descending fibers that derive from primary motor cortex. Recent studies have highlighted the functional role of these interactions in priming downstream elements for the ensuing motor actions. Time-resolved analysis has further emphasized the dynamic properties of pre-movement preparatory activity.


Spinal neurons operate as a processing link that integrates descending and peripheral information and in turn, generates a specific yet complex muscle command. The functional organization of spinal circuitry during normal motor behavior dictates the way in which this translation process is achieved. Nonetheless,
little is known about this organization during normal motor behavior. We examined the spatial organization of neural activity in the cervical spinal cord of behaving primates performing an isometric wrist task by estimating the averaged intraspinal activity of neuronal populations. We measured population response profiles and frequency content around torque onset and tested the tendency of these profiles to exhibit a specific organization within the spinal volume. We found that the spatial distribution of characteristic response profiles was non-uniform; namely, sites with a specific response profile tended to have a preferred spatial localization. Physiologically, this finding suggests that specific spinal circuitry that controls a unique feature of motor actions (with a particular task-related response pattern) may have a segregated spinal organization. Second, attempts to restore motor function via intraspinal stimulation may be more successful when the spatial distribution of these task-related profiles is taken into account.

2009


The basal ganglia network is divided into two functionally related subsystems: the neuromodulators and the main axis. It is assumed that neuromodulators adjust cortico-striatal coupling. This adjustment might depend on the response properties and temporal interactions between neuromodulators. We studied functional interactions between simultaneously recorded pairs of neurons in the basal ganglia while monkeys performed a classical conditioning task that included rewarding, neutral, and aversive events. Neurons that belong to a single neuromodulator group exhibited similar average responses, whereas main axis neurons responded in a highly diverse manner. Dopaminergic neuromodulators transiently increased trial-to-trial (noise) correlation following rewarding but not aversive events, whereas cholinergic neurons of the striatum decreased their trial-to-trial correlation. These changes in functional connectivity occurred at different epochs of the trial. Thus, the coding scheme of neuromodulators (but not main axis neurons) can be viewed as a single-dimensional code that is further enriched by dynamic neuronal interactions.

2008


Oscillatory bursting activity is commonly found in the basal ganglia (BG) and the thalamus of the parkinsonian brain. The frequency of these oscillations is often similar to or higher than that of the parkinsonian tremor, but their relationship to the tremor and other parkinsonian symptoms is still under debate. We studied the frequency dependency of information transmission in the cortex-BG and cortex-periphery loops by recording simultaneously from multiple electrodes located in the arm-related primary motor cortex (MI) and in the globus pallidus (GP) of two vervet monkeys before and after 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine (MPTP) treatment and induction of parkinsonian symptoms. We mimicked the parkinsonian bursting oscillations by stimulating with 35 ms bursts given at different frequencies through microelectrodes located in MI or GP while recording the evoked neuronal and motor responses. In the normal state, microstimulation of MI or GP does not modulate the discharge rate in the other structure. However, the functional-connectivity between MI and GP is greatly enhanced after MPTP.
treatment. In the frequency domain, GP neurons usually responded equally to 1-15 Hz stimulation bursts in both states. In contrast, MI neurons demonstrated low-pass filter properties, with a cutoff frequency above 5 Hz for the MI stimulations, and below 5 Hz for the GP stimulations. Finally, muscle activation evoked by MI microstimulation was markedly attenuated at frequencies higher than 5 Hz. The low-pass properties of the pathways connecting GP to MI to muscles suggest that parkinsonian tremor is not directly driven by the BG 5-10 Hz burst oscillations despite their similar frequencies.


It was suggested previously that the transformation of action to muscle-based coding is completed in the primary motor cortex (M1). This is consistent with a predominant direct pathway leading from M1 to motoneurons. Accordingly, spinal segmental interneurons that are located downstream to M1 are expected to show muscle-like coding properties. We addressed this hypothesis using simultaneous recording of cortical and spinal activity in primates performing an isometric wrist task with multiple targets and two hand postures. Here we show that while the motor cortex follows an intermediate coordinate frame, spinal interneurons already follow a muscle-like coordinate frame. We thus suggest that the final steps in coordinate transformation of motor commands take place downstream of M1 via corticospinal interactions.


Performing voluntary motor actions requires the translation of motor commands into a specific set of muscle activation. While it is assumed that this process is carried out via cooperative interactions between supraspinal and spinal neurons, the unique contribution of each of these areas to the process is still unknown. Many studies have focused on the neuronal representation of the motor command, mostly in the motor cortex. Nonetheless, to execute these commands there must be a mechanism that can translate this representation into a sustained drive to the spinal motoneurons (MNs). Here we review different candidate mechanisms for activating MNs and their possible role in voluntary movements. We discuss recent studies which directly estimate the contribution of segmental INs to the transmission of cortical command to MNs, both in terms of functional connectivity and as a computational link. Finally, we suggest a conceptual framework in which the cortical motor command is processed simultaneously via MNs and INs. In this model, the motor cortex provides a transient signal which is important for initiating new patterns of recruited muscles, whereas the INs translate this command into a sustained, amplified and muscle-based signal which is necessary to maintain ongoing muscle activity.

2007


Corticospinal (CS) pathways provide the structural foundation for executing voluntary movements. Although the anatomy of these pathways is well explored, little is known about spinal decoding of parametric information transmitted via this route during voluntary movements. We addressed this question by simultaneously recording cortical and spinal activity in primates performing an isometric wrist task with
multiple targets while measuring CS interactions. Single-pulse cortical stimulation effectively produced a short-latency (presumably monosynaptic) spinal response and thus revealed functionally connected CS sites. Spinal and cortical neurons recorded from connected CS sites showed alignment of directional-torque tuning that peaked at torque onset, consistent with the enhanced cortical drive active during this period. This increased tuning similarity was accompanied by an increased trial-to-trial covariability of firing. Whereas functional CS interactions were dynamic, the efficacy of cortical stimulation was unaffected by the motor state. These results suggest that around the onset of motor action there is a period of facilitated information transfer during which cortical command has greater efficacy in recruiting spinal neurons with matching tuning properties. Dynamic alignment of response properties may form the basis for a spinal readout mechanism of descending motor commands in which directional-torque is a parameter that is preserved across interacting CS sites.

2003


The firing properties of single spinal interneurons (INs) were studied in five awake, behaving monkeys performing isometric or auxotonic flexion-extension torques at the wrist. INs tended to fire tonically at rest (mean rate, 14 spikes (sp)/sec) and during generation of static torque (mean rate, 19 sp/sec in flexion, 24 sp/sec in extension). INs exhibited regular firing, with autocorrelation functions showing clear periodic features and a mean coefficient of variation of interspike intervals (CV) of 0.55 during production of static torque. For the population, there was an inverse correlation between CV and mean rate. However, 46% of the INs had task-dependent changes in regularity that were not predicted by changes in firing rate, suggesting that their firing pattern is determined not only by the intrinsic properties of the neurons but also by the properties of its synaptic inputs. INs showed two main response types to passive wrist displacement: biphasic and coactivation. Cells with these sensory responses had different, stereotypical temporal activity profiles and firing regularity during active movement. However, INs having correlational linkages with forearm muscles, identified as features in spike-triggered averages of electromyographic activity, did not exhibit unique responses or firing properties, although they tended to fire more regularly than other INs. This suggests the lack of a precise mapping of inputs to outputs for the spinal premotor network.


The relationship between the activity of pairs of simultaneously recorded spinal interneurons (INs) in the cervical enlargement was studied in five monkeys performing voluntary wrist movements. The tendency for INs to exhibit similar response properties and synchronized firing was tested as a function of physical distance between the cells and their correlational linkages with forearm muscles. Nearby INs tended to have more similar torque and direction turning (signal correlation) and more similar response profiles (e.g., tonic vs phasic firing) than INs that were far apart. This suggests that nearby cells receive common synaptic input. In contrast, the trial-to-trial covariation of rate around the mean rate for all trials (noise correlation) was independent of the distance between the neurons. Furthermore, signal and noise
correlation were independent, suggesting different underlying mechanisms. Surprisingly, spike-to-spike correlation between INs was relatively infrequent and weak, as measured by cross-correlation histograms. In contrast, single motor units (SMUs) in forearm muscles fired more synchronously, particularly for SMUs in single extensor muscles. Either common drive to INs is too weak to induce synchronized firing, or there is an active decorrelation mechanism within IN networks.

2002


To study the contribution of primate cervical interneurons (INs) to preparation and execution of normal voluntary hand movement we investigated their activity and correlational linkages to muscles in monkeys performing tracking tasks. During ramp-and-hold flexion-extension torques about the wrist most task-related spinal INs exhibited some activity during both flexion and extension, in unexpected contrast to the strictly unidirectional activity of corticomotoneuronal (CM) cells and motoneurons. Most INs increased their activity more in one of these two directions; response patterns in their preferred direction were typically tonic or phasic-tonic. Spike-triggered averages of EMG detected significant features in muscle activity for many task-related INs. Premotor INs (PreM-INs) were identified by post-spike facilitation or suppression with appropriate onset latencies after the trigger spike. Muscle fields of PreM-INs were smaller than those of supraspinal PreM cells in cortex and red nucleus, and rarely involved reciprocal effects on antagonist muscles. To investigate the relation of spinal INs to a repertoire of different muscle synergies, activity of INs was recorded from a macaque performing a multidirectional wrist task. The monkey generated isometric torques in flexion/extension, radial/ulnar deviation, pronation/supination, and executed a power grip that co-contracted wrist flexor and extensor muscles. Many INs showing task-modulated activity had preferred directions in this multidirectional space, typically with broadly tuned activation. The role of spinal INs in preparation for voluntary movement was revealed in monkeys performing instructed delay tasks. During the delay between a transient visual cue and a go signal a third of the tested INs showed significant delay modulation (SDM) of firing rate relative to the pre-cue rate. The SDM responses often differed from the INs’ responses during the subsequent active torque period. In a monkey instructed by either visual or proprioceptive cues the delay period activity for many INs was similar in visual and perturbation trials, although other INs exhibited different SDM for visually and proprioceptively cued trials. These results suggest that spinal INs are involved, with cortex, in the earliest stages of movement preparation. The sensory input to INs could be identified in transient responses to the torque pulse, which showed two predominant patterns, consistent with inputs from cutaneous or proprioceptive receptors. We also investigated the task-dependent modulation of neural responses to peripheral input in a monkey performing wrist flexion/extension movements in a visually cued instructed delay task. Monosynaptic responses evoked by electrical stimulation of the superficial radial nerve through a cuff electrode were suppressed or abolished during the dynamic movement phase. Since task-related activity of the INs increased at the same time, the suppression was mediated by presynaptic rather than postsynaptic inhibition. These observations indicate that under normal behavioral conditions many spinal INs have response properties comparable to those previously documented for cortical neurons in behaving animals.

The activity of cervical spinal interneurones (INs) was recorded in monkeys performing alternating hand movements. The contribution of INs to voluntary movement was determined by their response patterns during ramp-and-hold wrist movements and their postspike effects on forelimb muscle activity. Most INs were active during both flexion and extension, in contrast to the unidirectional activity of muscles and corticomotoneuronal cells. When recorded during performance of an instructed delay task, the activity of many INs was modulated during the delay period between the instruction cue and the subsequent go signal. Thus, spinal INs, like cortical neurones, participate in earliest stages of preparation for movement.

The modulation of peripheral input to spinal INs was tested during an instructed delay task. The monosynaptic responses to electrical stimulation of a cutaneous nerve decreased during active movement, probably due to presynaptic inhibition. These results provide new insights into the role of spinal INs in preparation and execution of voluntary movement.

2001


Recordings of spinal INs during a flexion/extension wrist task with an instructed delay period have shown directly that many spinal neurons modulate their rate during the preparatory period soon after a visual cue. The onset time and the relation between the delay period activity of spinal INs and the ensuing movement response suggest that this type of activity is not simply related to the forthcoming motor action, but rather reflects a correct match between the visual cue and the motor response. The existence of such activity further supports the notion that the motor system operates in a parallel mode of processing, so that even during early stages of motor processing multiple centers are activated regardless of their anatomical distance from muscles. The firing properties of spinal INs during the performance of the task seem to differ from the comparable properties of motor cortical cells. Spinal INs fire in a highly regular manner--their CV is substantially lower than the observed CV of cortical cells. Also, although neighboring cells tend to have similar response properties, the frequency of significant correlation is lower than for cortical cells and the anatomical extent of the correlation seems to be narrower. The similarity and differences between cortical and spinal cells in terms of response and firing properties suggests that while both type of cells are active in parallel throughout the behavioral phases of the motor task, each may operate in a different mode of information processing.

2000


The major recent advances in understanding the role of spinal neurons in generating movement include new information about the modulation of classic reflex pathways during fictive locomotion and in response to pharmacological probes. The possibility of understanding movements in terms of spinal representations of a basic set of movement primitives has been extended by the analysis of normal reflexes. Recordings of the activity of cervical interneurons in behaving monkeys has elucidated their contribution to generating
voluntary movement and revealed their involvement in movement preparation.

1999


Abstract

There is considerable overlap between the cognitive deficits observed in humans with frontal lobe damage and those described in patients with Parkinson's disease. Similar frontal impairments have been found in the 1-methyl-4-phenyl-1,2,3, 6-tetrahydropyridine (MPTP) primate model of Parkinsonism. Here we provide quantitative documentation of the cognitive, oculomotor, and skeletomotor dysfunctions of monkeys trained on a frontal task and treated with low-doses (LD) of MPTP. Two rhesus monkeys were trained to perform a spatial delayed-response task with frequent alternations between two behavioral modes (GO and NO-GO). After control recordings, the monkeys were treated with one placebo and successive LD MPTP courses. Monkey C developed motor Parkinsonian signs after a fourth course of medium-dose (MD) MPTP and later was treated with combined dopaminergic therapy (CDoT). There were no gross motor changes after the LD MPTP courses, and the average movement time (MT) did not increase. However, reaction time (RT) increased significantly. Both RT and MT were further increased in the symptomatic state, under CDoT. Self-initiated saccades became hypometric after LD MPTP treatments and their frequency decreased. Visually triggered saccades were affected to a lesser extent by the LD MPTP treatments. All saccadic parameters declined further in the symptomatic state and improved partially during CDoT. The number of GO mode (no-response, location, and early release) errors increased after MPTP treatment. The monkeys made more perseverative errors while switching from the GO to the NO-GO mode. Saccadic eye movement patterns suggest that frontal deficits were involved in most observed errors. CDoT had a differential effect on the behavioral errors. It decreased omission errors but did not improve location errors or perseverative errors. Tyrosine hydroxylase immunohistochemistry showed moderate (approximately 70-80%) reduction in the number of dopaminergic neurons in the substantia nigra pars compacta after MPTP treatment. These results show that cognitive and motor disorders can be dissociated in the LD MPTP model and that cognitive and oculomotor impairments develop before the onset of skeletal motor symptoms. The behavioral and saccadic deficits probably result from the marked reduction of dopaminergic neurons in the midbrain. We suggest that these behavioral changes result from modified neuronal activity in the frontal cortex.


1998

The study was designed to reveal occurrences of precise firing sequences (PFSs) in cortical activity and to test their behavioral relevance. Two monkeys were trained to perform a delayed-response paradigm and to open puzzle boxes. Extracellular activity was recorded from neurons in premotor and prefrontal areas with an array of six microelectrodes. An algorithm was developed to detect PFSs, defined as a set of three spikes and two intervals with a precision of +/-1 ms repeating significantly more than expected by chance. The expected level of repetition was computed based on the firing rate and the pairwise correlation of the participating units, assuming a Poisson distribution of event counts. Accordingly, the search for PFSs was corrected for rate modulations. PFSs were found in 24/25 recording sessions. Most PFSs (76%) were composed of spikes of more than one unit but usually not more than two units (67%). The PFSs spanned hundreds of milliseconds, and the average interval between two events within the PFSs was 200 ms. No traces of periodic oscillations were found in the PFS intervals. The bins of the matrix that were defined as PFSs were isolated temporally: the spikes that generated PFSs were not associated with high-frequency bursts or rapid coherent rate fluctuations. A given PFS tended to be correlated with the animal's behavior. Furthermore, for 19% of the PFS pairs that shared the same unit composition, each member of the pair was associated with a different type of behavior. The PFSs often appeared in clusters that were associated with particular phases of the behavior. The firing rate of single units did not provide a full explanation for the timing and structure of these clusters. A reduced spike train (RST) was defined for each unit by taking all spikes of that unit that were part of any PFS. In 88% of the cases the degree of modulation of the RST was higher than that of the complete spike train. The results suggest that relevant information is carried by the fine temporal structure of cortical activity. A coding scheme that involves such temporal structures is rich and sufficiently flexible to facilitate a rapid organization of cortical neurons into functional groups. The results can be accounted for by the synfire chain model, which suggests that cortical activity is mediated by synchronous activation of neural groups in a reverberatory mode.

1996


Recording the activity of several neurons in parallel in the frontal cortex of behaving monkeys reveals that firing times of neurons can maintain +/- 1 ms accuracy even after delays of over 400 ms. The accurate firing structures were associated with behavior. Neural networks that can sustain such accuracy can learn 'learn' to bind with each other and thus may serve as building blocks for cognitive processes.

1995


It is possible that brain cortical function is mediated by dynamic modulation of coherent firing in groups of neurons. Indeed, a correlation of firing between cortical neurons, seen following sensory stimuli or during motor behaviour, has been described. However, the time course of modifications of correlation in relation
to behaviour was not evaluated systematically. Here we show that correlated firing between single
neurons, recorded simultaneously in the frontal cortex of monkeys performing a behavioural task, evolves
within a fraction of a second, and in systematic relation to behavioural events. Moreover, the dynamic
patterns of correlation depend on the distance between neurons, and can emerge even without modulation
of the firing rates. These findings support the notion that neurons can associate rapidly into a functional
group in order to perform a computational task, at the same time becoming dissociated from concurrently
activated competing groups. Thus, they call for a revision of prevailing models of neural coding that rely
solely on single neuron firing rates.

1994

Nelken, I, Prut Y, Vaadia E, Abeles M. 1994 In search of the best stimulus: an optimization procedure

Units in the auditory cortex of cats respond to a large variety of stimuli: pure tones, AM- and FM-modulated
signals, clicks, wideband noise, natural sounds, and more. However, no single family of sounds was found
to be optimal (in the sense that oriented lines are optimal in the visual cortex). The search for optimal
complex sounds is hard because of the high dimensionality of the space of interesting sounds. In an effort
to overcome this problem, an automatic search procedure for finding efficient stimuli in high-dimensional
sound spaces was developed. This procedure chooses the stimuli to be presented according to the
responses to past stimuli, trying to increase the strength of the response. The results of applying this
method to recordings of population activity in the primary auditory cortex of cats are described. The search
was applied to single tones, two-tone stimuli, four-tone stimuli and to a two-dimensional subset of nine-tone
stimuli, parametrized by the center frequency and the fixed difference between adjacent frequencies.
The method was able to find efficient stimuli, and its performance improved with the dimension of the
sound spaces. Efficient stimuli, found in different optimization runs using population activity recorded from
the same electrode, often shared similar frequencies and pairs of frequencies, and tended to evoke similar
levels of activity. This result indicates that a global analysis of the location of spectral peaks is performed at
the level of the auditory cortex.

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