Stimulus specific processing within different auditory regions of the songbird brain during a variety of listening tasks: Evidence from the BOLD response

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Introduction

Songbirds evolved the remarkable feature of vocal communication, with an underlying learning behavior which is very familiar to human speech and language. The recent successful application of BOLD fMRI in songbirds exposed to acoustic stimuli (Van Meir et al, 2003), spanning the broad range of sensory motor complexity and different levels of cognitive processing, provides a potential path for bridging the gap between the basic experimental stimuli, often applied in rats and mice, and the real-world behavior of small laboratory animals, even under anaesthetized conditions. Furthermore, it may establish a link between human neuroimaging studies done on auditory and language processing, and the large body of neuroethological research performed in songbirds over the last few decades. Considering the novelty of the songbird as a model in fMRI and given the known differences in molecular and electrophysiological responses between auditory regions and acoustic stimuli, we explored the shape of the BOLD response as a function of different auditory tasks in three auditory regions: (1) Field L, which can be compared with the mammalian auditory cortex, (2) the caudomedial neostriatum (NCM), a secondary auditory region involved in the processing of species specific acoustic features, and (3) the nucleus ovoidalis (Ov), the thalamic auditory relay center in songbirds. It was our aim to discern the differential neuronal processing strategies in the auditory system of song birds and to improve post processing methods to discriminate adjacent activated auditory regions.

Methods

6 adult male Starlings were anaesthetized with a mixture of ketamine (Ketalar) and methodomidine (Domitor) (Van Meir et al, 2003). Their heads were positioned in a custom made stereotaxic device, leaving the ears free for auditory stimulation with a dynamic speaker positioned next to each ear at a distance of approximately 1 cm. Two slices with FOV=30 mm, slice thickness=700 µm and acquisition matrix=128x64, covering the telencephalic and thalamic auditory regions in the right brain hemisphere, were imaged on a 7T MRRS system (UK), using a GE-FLASH sequence (TE/TR=14/80 ms). Application of long gradient ramp times (1000 µsec) reduced the noise of the system to 80 dB. Auditory stimuli were provided at 100 dB using a classical block design with 14 alternating stimulation and rest periods of 1 minute each; during each block 24 images were acquired. Stimulation types were white noise, a concerto of Bach and conspecific song. The latter two were presented either as an entire sequence for one minute or in a segmented fashion, where the same fragment was repeated with the acquisition of each image during the stimulation period**.** Images were reconstructed to a 128x128 matrix (MRRS software), resulting in an in plane resolution of 230 µm, and post processed by spatial smoothing with a 0.7 mm (3 pixels) full-with-at-half-maximum Gaussian kernel and normalization to a whole image mode value of 1000 (MedX). The % signal intensity (SI) change within 3 ROI's of 6 pixels positioned in Field L, NCM and Ov were compared for the different stimulation types using a 3 way repeated measures ANOVA with the 5 stimulation types, the 14 blocks, and the 24 time points per block as repeated measures.

Results

A significant effect was found for the % SI change during stimulation and rest in all regions. Inspection of the mean BOLD response to all stimuli as presented in figure 1 (first column) shows that for each region a specific BOLD response can be observed that reaches a maximum during the first five to ten seconds of the stimulation and in the telencephalon reaches to a steady state during the last 30 seconds of the stimulation period. Immediately after the end of the stimulus a significant dip in the response is observed followed by a relaxation to baseline.

The analysis indicated that the shape of the BOLD response was specific for each stimulation (significant interaction between stimulus type and % SI change) within each region as can be seen in the three last columns of figure one.

The differences in response over the different brain regions seems to be related to complexity and behavioral relevance of the stimulus, with the conspecific song being both behaviorally relevant and complex, the concerto of Bach only complex and white noise least complex. The repeated fragments of song and Bach music represent an intermediate situation. In field L every stimulation type leads to a transient response. In NCM, responses tend to be more sustained and the amplitude changes with complexity, giving no response at all to white noise. Behavioral relevance of the stimulus seems to be positively related with the amplitude of the response in both field L and NCM. In Ov, the thalamic relay center that provides input to field L and receives projections from the higher order processing regions such as NCM, exactly the opposite is observed: highest response during white noise stimulation and no response during conspecific song.

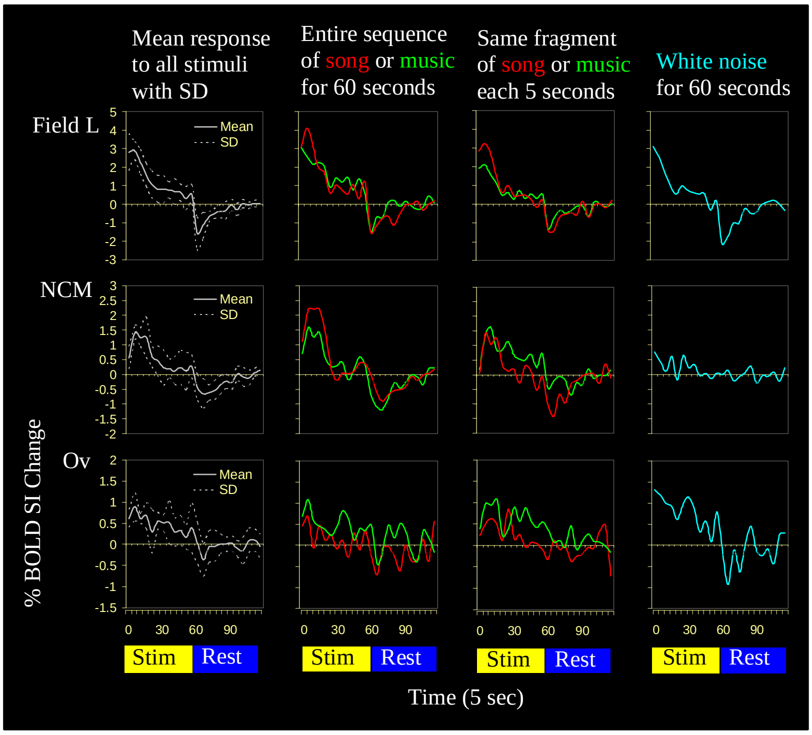

Figure 1: Illustration of the BOLD response in three auditory regions to a variety of acoustic stimuli. The left column shows the mean BOLD response of all stimuli in each region. The three next columns show the BOLD response to each stimulus separate. The complexity of the stimuli decreases from the left to the right column
The response to conspecific song and its fragmented version is shown in red, whereas the response to the concerto of Bach is presented in green. The timescale of 5 seconds represents the acquisition time of one image.

Discussion

We can conclude that the shape of the BOLD response is region and stimulus specific. Within the telencephalon, a transient response, as seen in field L, might indicate sensory information processing whereas a sustained response, as present in NCM, might indicate a more cognitive process (D' Avossa et al., 2003). Temporal aspects of the BOLD response could be important features to reveal functional connectivity such as bottom-up and top-down processes, which results in a different complexity of neural activity within one region during different tasks leading to a change in the shape of the BOLD response or even a suppression as seen in Ov.

References

1. Van Meir V. et al., 2003, abstract on the annual ISMRM meeting, ID 3078
2. D' Avossa G. et al., 2003, J Neurophysiol. 90: 360-371