Hearing Research 344 (2017) 1–12

Contents lists available at ScienceDirect

Hearing Research

journal homepage: www.elsevier.com/locate/heares

Research Paper

Spatial and temporal disparity in signals and maskers affects signal detection in non-human primates

Francesca Rocchi, Margit E. Dylla, Peter A. Bohlen, Ramnarayan Ramachandran*

Department of Hearing and Speech Sciences, Vanderbilt University Medical Center, Nashville, TN 37212, USA

ARTICLE INFO

Article history:
Received 22 February 2016
Received in revised form
10 October 2016
Accepted 15 October 2016
Available online 19 October 2016

Keywords:
Detection threshold
Auditory scene analysis
Temporal asynchrony
Spatial release from masking
Auditory masking

ABSTRACT

Detection thresholds for auditory stimuli (signals) increase in the presence of maskers. Natural environments contain maskers/distractors that can have a wide range of spatiotemporal properties relative to the signal. While these parameters have been well explored psychophysically in humans, they have not been well explored in animal models, and their neuronal underpinnings are not well understood. As a precursor to the neuronal measurements, we report the effects of systematically varying the spatial and temporal relationship between signals and noise in macaque monkeys (*Macaca mulatta* and *Macaca radiata*). Macaques detected tones masked by noise in a Go/No-Go task in which the spatiotemporal relationships between the tone and noise were systematically varied. Masked thresholds were higher when the masker was continuous or gated on and off simultaneously with the signal, and lower when the continuous masker was turned off during the signal. A burst of noise caused higher masked thresholds if it completely temporally overlapped with the signal, whereas partial overlap resulted in lower thresholds. Noise durations needed to be at least 100 ms before significant masking could be observed. Thresholds for short duration tones were significantly higher when the onsets of signal and masker coincided compared to when the signal was presented during the steady state portion of the noise (overshoot). When signal and masker were separated in space, masked signal detection thresholds decreased relative to when the masker and signal were co-located (spatial release from masking). Masking release was larger for azimuthal separations than for elevation separations. These results in macaques are similar to those observed in humans, suggesting that the specific spatiotemporal relationship between signal and masker determine threshold in natural environments for macaques in a manner similar to humans. These results form the basis for future investigations of neuronal correlates and mechanisms of masking.

1. Introduction

Background sounds often result in an increase in threshold levels for detecting signals. In the real world, maskers may occur in complex spatiotemporal configurations relative to the signal to be detected. The auditory system relies on temporal, spectral and spatial cues to detect s in noise. Low-level features, such as the signal onset and the spatial location of sound energy, represent important cues for signal detection and formation of auditory scenes (Bregman, 1990). Here we report the results of studies investigating how the spatio-temporal properties of background noise affect masking.

Behavioral and neuronal responses to a target sound are sensitive to other sounds that occur around the time of occurrence of the target sound. Not surprisingly, masked detection is sensitive to the temporal structure of the target signal and the masker. Behaviorally, these have been best exemplified by studies of simultaneous masking, and studies of forward and backward masking (non-simultaneous masking), which involve manipulations of stimulus onset asynchrony of maskers and signals (e.g. de Maré, 1940; Lüscher and Zwislocki, 1947; Munson and Gardner, 1950; Zwislocki et al., 1959; Plomp, 1964; Elliott, 1971; Widin and Viemeister, 1979; Jesteadt et al., 1982; Moore and Glasberg, 1983; Nelson, 1991; Plack and Oxenham, 1998). The behavioral consequences of such temporal relationships have not been well studied

* Corresponding author. Department of Hearing and Speech Sciences, Vanderbilt University Medical Center, 111 21st Ave S, WH 065, Nashville, TN 37212, USA
E-mail address: ramnarayan.ramachandran@vanderbilt.edu (R. Ramachandran).

http://dx.doi.org/10.1016/j.heares.2016.10.013
0378-5955/

in animal models that will directly allow exploration of neuronal mechanisms. Inhibition/suppression, neuronal adaptation, inhibition or forward suppression, and offset inhibition are all mechanisms that have been proposed to contribute to simultaneous and non-simultaneous masking (e.g. Duifhuis, 1973; Nelson and Swain, 1996; Oxenham and Moore, 1995, 1997; Harris and Dallos, 1979; Brosch and Schreiner, 1997; Gai, 2016).

It is well known that the relative locations of signals and maskers/distractors strongly influence audibility of the target signal (e.g., Santon, 1987). Separation of target signal and masker/distractor in azimuth and/or elevation can cause detection thresholds to be lower by 10–12 dB (spatial release from masking, Saberi et al., 1991). While much of this work has been done in humans, to the best of our knowledge there are no studies in nonhuman animal models that address spatial effects of maskers and distractors on masked detection (however see Sollini et al., 2016). Most of the work done in humans using free field sounds has mainly focused on speech intelligibility (e.g. Plomp, 1976; Plomp and Mimpen, 1981). Only a few studies (e.g. Santon, 1987; Gatehouse, 1986, 1987; Kidd et al., 1998; Saberi et al., 1991) of masking using tones and noise have been conducted in a free field. This study extends the spatial release in masking literature to animal models; here, the benefit of spatial separation of signal and noise on detection threshold (audibility) is directly addressed.

In this study, we explored the effect of varying spatial and temporal relationships between a signal and a masker in free field on masked signal detection. Although spatial and temporal release from masking have been extensively studied in humans, they have not been well explored in animal models that permit direct exploration of the neuronal mechanisms underlying these phenomena, especially in macaques. The use of non-human primates as behavioral model in hearing research has increased over the last decade (e.g., O'Connor et al., 2011; Osmanski et al., 2013; Dylla et al., 2013; Christison-Lagay and Cohen, 2014). The similarity in behavioral performance across human and nonhuman primate species observed in many of the above studies suggests that nonhuman primates may be a good model for human hearing; phylogenetic similarity suggests that the neuronal mechanisms underlying behavioral performance may be similar across these two species. While macaques are being increasingly used in behavioral and physiological studies of the auditory system, there are very few studies on masking. We used macaques to obtain behavioral results for factors influencing masked detection; these provide a baseline for planned investigations of neuronal mechanisms underlying hearing in more naturalistic environments, in which signals and maskers may have spatial and temporal disparities. These also form a baseline for studies of the consequences of hearing impairment.

2. Methods

2.1. Subjects

Five male macaque monkeys (four *Macaca mulatta* and one *Macaca radiata*) were used as subjects. Monkeys A, B, C and D (*Macaca mulatta*) were 10, 9, 7 and 6 years old, respectively at the start of the study, while Monkey G (*Macaca radiata*) was 7 years old. All monkeys showed audiometrically normal hearing thresholds measured (in dichotic conditions) over the range of frequencies spanning 0.125–40 kHz (Dylla et al., 2013; Bohlen et al., 2014). All the procedures were approved by the Animal Care and Use Committee of the Vanderbilt University Medical Center and were strictly consistent with the guidelines for animal research established by the National Institutes of Health.

2.2. Surgical procedure

Monkeys were prepared for chronic experiments using standard techniques employed in previous studies (e.g. Ramachandran and Lisberger, 2005; Dylla et al., 2013). The surgical procedure was performed prior to the behavioral tasks. A metal head holder (Crist Instruments, Hagerstown, MD) was placed on the skull of the monkeys to maintain the position of their head at a constant location with respect to the loudspeakers. Bone cement and eight-mm-long stainless steel screws (Synthes Inc., and Veterinary Orthopedic Instruments) were used to secure the head post to the skull. Analgesics, and if necessary, antibiotics were administered to the monkeys under veterinary oversight. Further details about the surgical procedures are given in Dylla et al. (2013).

2.3. Apparatus and stimuli

Experiments were conducted in a sound treated booth (model 1200, Industrial Acoustics Corp., NY or Acoustic Systems) where the monkeys were seated in an acrylic primate chair (audio chair, Crist Instrument Co., Hagerstown, MD). The holder implanted on the monkeys' skull was fastened to the chair. The distance between the loudspeakers and the head of the monkeys varied depending on the task used (for details, see *behavioral task* section). Sounds between 0.05 and 40 kHz (SA1 loudspeaker, Madisound, WI) could be delivered by the loudspeakers, whose on-axis output varied less by than 3 dB between 100 Hz and 40 kHz. A microphone placed at the location of one of the monkey's head was used for calibration. Loudspeakers were further calibrated at different spatial locations to ensure that the sound level at the ear canal was the same irrespective of spatial location.

A computer running OpenEx software (System 3, TDT Inc., Alachua, FL controlled the experiments. The sampling rate used to generate the signals (tones and noise) was 97.6 kHz. The lever state was sampled at a rate of 24.4 kHz, leading to a temporal resolution of about 40 μs on the lever release. A full description of the apparatus used to generate the signals and masker is provided in Dylla et al. (2013).

2.4. Behavioral task and procedure

Monkeys were trained to release a lever to report detection of a tone in noise with positive reinforcement. Detection performance was measured only when the monkeys consistently performed the task. The behavioral procedures are described in Dylla et al. (2013) and Bohlen et al. (2014). Briefly, all trials started with the monkeys pressing down on the lever (Model 829 Single Axis Hall Effect Joystick, P3America, San Diego, CA). The signal (tone) was presented after a variable delay (400–1400 ms) following the lever press. A fluid reward was given each time the tone was correctly detected (hit) by releasing the lever within 600 ms of the tone onset. No penalty was given when a tone was presented but the monkey did not release the lever (miss). 80% of trials included a tone, and the remaining 20% no tone was played (catch trials). When the lever was released but a tone was not played (false alarm), a time-out penalty was applied (tones were not presented for a variable time between 6 and 10 s). The step size between tone levels was either 2.5 or 5 dB. Tone levels were chosen from a range spanning 90 dB. The method of constant stimuli was applied with randomized presentation order of each level, and each level was used a minimum of 15 and a maximum of 30 times. A specific masker was chosen for each block. The spatial and temporal properties of noise relative to the tone are specific to the experiment and are described in the appropriate