Neuronal responses to visual stimuli in auditory cortical areas of monkeys performing an audio-visual detection task.

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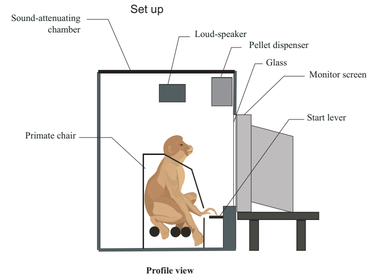
Introduction

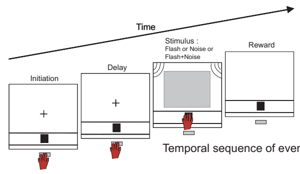
On the psychophysical point of view, as compared to unimodal stimuli, multisensory integration allows improvement of perceptive threshold, as reflected by a decrease of reaction time and better performance in sensori-motor tasks. While such effects have been largely reported for human subjects in auditory-visual recognition tasks, only few data are available in behaving monkeys engaged in similar protocols. Multisensory integration is believed to take place mainly in higher order cortical areas. On a behavioral point of view, we have investigated the interaction between auditory and visual stimuli in monkeys. Moreover, the present study aimed at exploring the mechanisms underlying multisensory integration at the level of single neurons during a multisensory motor task in a cortical region considered as unimodal, a dimension that cannot be assessed in human subjects.

Methods

Stimuli for electrophysiological recordings

Visual stimuli : flash on the screen in front of the animal (9.2 Lux).
Auditory stimuli : noise burst delivered from 2 loudspeakers on each side of the screen (40 or 60 dB SPL). The duration of stimuli was 250 ms.

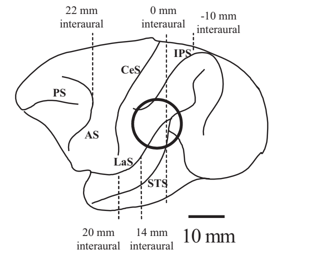




Temporal sequence of events during a typical trial

Two adult Macaca fascicularis were trained to perform a visuo-acoustic detection task. To initiate a trial, the monkey has to place his left hand on a starting pad, the fixation point on the monitor facing the monkey is turned on and the monkey has to fixate during the entire trial. The initiation of the trial is followed by a random delay. Then, the sensory cue is presented, consisting of a unimodal **visual (V)** or **auditory (A)** stimulus, or a bimodal **audio-visual (AV)** stimulus corresponding to the simultaneous presentation of the two individual cues. The sequence of unimodal (auditory or visual) or bimodal trials is random. In response to each stimulus, the monkey has to touch a pad just above the starting pad. If the motor response was given within a certain time window, the animal received the reward (pellet) and the reaction time (RT) was measured.

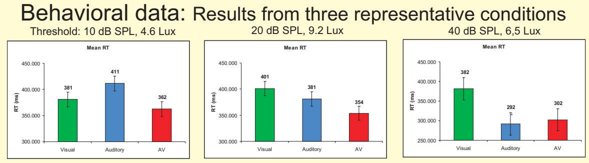
In parallel, in the same monkeys, electrophysiological recordings were derived from single neurons in the auditory cortex and adjacent cortical zones in the posterior bank of the lateral sulcus. Extracellular neuronal activity was recorded with tungsten microelectrodes (Frederick Haer and Co), advanced with a hydraulic microdrive (Narishige) attached to the recording chamber chronically fixed to the head of monkey. Cortical activity was recorded while the monkey performed the behavioral task. The control of the task and discrimination of neurons was done using the OpenEx software (Tucker-Davis-Technology (TDT), Florida, USA).



Location of the electrophysiological recording chamber on a lateral view of a macaque brain (left hemisphere). AS: arcuate sulcus, CeS: central sulcus, IPS: intraparietal sulcus, LaS: lateral (Sylvian) sulcus, PS: principal sulcus, STS: superior temporal sulcus.

Results

Behavioral data: Results from three representative conditions



Mean RT (+/-S.E.). *P<0.001 — Mean RT (+/-S.E.). *P<0.001 — Mean RT (+/-S.E.). *P<0.001, n.s=non significant

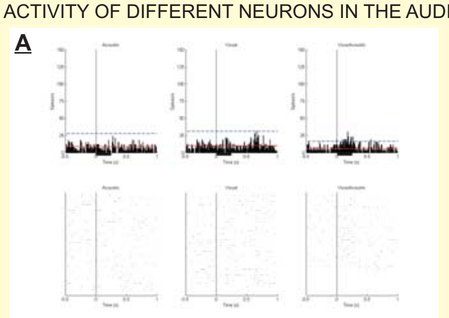
These results show that mean reaction times for multisensory conditions at 20 dB SPL, 9.2 Lux and 10 dB SPL, 4.6 Lux (i.e near threshold) were significantly faster than those for the corresponding unisensory conditions ; however this is not the case at 40 dB SPL, 6.5 Lux.

Electrophysiological recordings

The activity of 308 single neurons was recorded from the auditory cortex (in the large sense), from which **125** units exhibited a discharge pattern related to the behavioral task (responses to "**A**" and/or to "**V** and/or to "**A+V**"). The neuronal activity was represented in the form of dot raters and peri-event histograms (see below). We compared the mean spontaneous discharge rate (quantified in action potentials per second (PA/s)) with the mean discharge rate during the presentation of stimuli ("**A**", "**V**" or "**A+V**") using a t-test (significant difference if p<0.05). A further statistical assessment was provided in the peri-event histograms, with lines representing the mean spontaneous discharge rate (see red line below) and a deviation from the latter by +/- 2 SDs (see blue dashed line below).

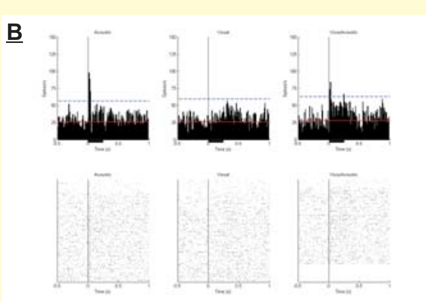
ACTIVITY OF DIFFERENT NEURONS IN THE AUDITORY CORTEX DURING A DETECTION TASK OF AUDITORY (A), VISUAL (V) AND AUDIO-VISUAL (AV) STIMULI

A

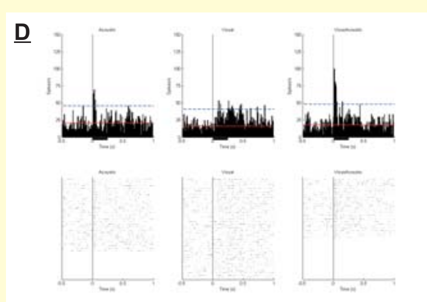


C

B



D



Categories of neurons in multisensory context

1: no multisensory interaction

1a. "Predominant Auditory unit": Resp. "A" = Resp "A+V" (no influence of "V")
n=35 (28%)

1b. "Predominant Visual unit": Resp. "V" = Resp "A+V" (no influence of "A")
n=53 (42.4 %)

1c. "No predominance": Resp. "A" = Resp. "V" = Resp "A+V"
n=2 (1.6 %)

2: simple multisensory sommation (predictible)

Resp "A+V" = Resp. "A" + Resp. "V" (responds to both modalities)
n=6 (4.8 %)

3: multisensory interaction (not predictible)

3a. Resp "A+V", but no response to "A" and no response to "V"
n=11 (8.8 %) **see Neuron A**

3b. Resp. "A", no Resp "V" but interaction between "A" and "V"
n=5 (4 %) **see Neuron B**

3c. Resp. "V", no Resp. "A" but interaction between "A" and "V"
n=6 (4.8 %) **see Neuron C**

3d. Resp "A" and Resp. "V" with interaction between "A" and "V"
n=7 (5.6 %) **see Neuron D**

Example of discharge pattern of 4 neurons (A, B, C and D) recorded in the posterior bank of the LaS. In the raster display (bottom panel), each dot corresponds to an action potential and each line of dots to a trial. Above the rasters, the activity is represented by the cumulated trials in the forms of PEH (peri-event histogram) in PA/s with 10 ms bindwidth. The trials are aligned on stimulus onset "Acoustic" (left column), "Visual" (medium column) or "VisuoAcoustic" (right column). Each stimulus lasts 250 ms, which is represented by the horizontal bar below the time scale. These 4 neurons illustrate the 4 types of multisensory interactions (see category #3 above, on the right).

Conclusion

On the behavioral point of view, the bimodal ("A"+"V") condition had a significant facilitatory effect on reaction times and stimulus detection near threshold and at moderate acoustic intensity; this effect disappeared at higher intensities.
On the electrophysiological point of view, different types of neuronal responses were observed. As expected, some neurons responded only to auditory stimuli. However, somewhat surprising, other neurons in the auditory cortex (in the large sense) were influenced also by visual stimuli. Thus, the auditory cortex contains neurons which respond both to auditory and visual stimuli. In addition, about a quarter of neurons exhibited a non-predictible multisensory interaction (complex influence of auditory stimuli on visual responses or of visual stimuli on auditory responses).

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