EVOKED UNIT ACTIVITY IN AUDITORY CORTEX OF MONKEYS
PERFORMING A SELECTIVE ATTENTION TASK

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SUMMARY

Single-unit responses were recorded from the auditory cortex of rhesus monkeys performing a selective attention task which used combined light and sound stimuli. The animals were first trained to push a lever to the left for a noise burst and to the right for a tone burst, and then trained to push left for a left light and right for a right light. Subsequently, one of the four possible light and sound stimulus combinations (Noise + Left Light, Noise + Right Light, Tone + Left Light, Tone + Right Light) was randomly presented on each trial. In blocks of 100 trials only one part of the combined stimulus (either the light or the sound) determined the direction of lever push that would be reinforced. Responses of single units to identical sound stimuli were compared for blocks in which sound was the relevant cue and blocks in which light was the relevant cue. Typically, differences were in response strength without alteration of response pattern. Even the earliest response components (15–20 msec latency) could show changes. Two-thirds of the response comparisons showed differences in strength depending upon whether sound or light was the relevant cue, with about as many responses stronger for light relevant as for sound relevant. Independent of which modality was relevant, unit responses for trials in which both parts of the combined light and sound stimulus indicated the same direction of lever push were generally stronger than unit responses for trials in which the two parts of the combined stimulus signalled opposite directions of lever pushes.

INTRODUCTION

The stimulus-encoding properties of the auditory cortex have been extensively

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studied by techniques employing single-unit or evoked potential recording\textsuperscript{1,4,5,7,9–11, 18,20,22}. These techniques have for the most part required the use of an anesthetized or muscle-relaxed preparation. With the increasing use of procedures involving recording from awake, non-paralyzed, behaviorally-trained animals it is becoming evident that the behavioral state of the animal can influence neural activity in the auditory cortex.

It has been reported that the evoked responses of single-units in the auditory cortex of monkeys can be modified by requiring the animal to perform an auditory task\textsuperscript{13} and further, by changing the contingencies of reinforcement in an auditory task\textsuperscript{5}. The results from these two studies raise the question of whether changes in unit responsiveness in the auditory cortex are limited to the performance of tasks which involve the discrimination of auditory cues. Our aim was to study the question by using a task with combined light and sound stimuli which would require an animal to selectively attend to the sound cues under one condition and to selectively attend to the light cues under the other condition. Our principal data were the comparisons of unit responses to identical acoustic stimuli under the two conditions in which either sound or light was the relevant cue for performing the task.

METHODS

Behavioral paradigm and training

Six rhesus monkeys (Macaca mulatta) were trained on the discrimination tasks using water as the reinforcer. During training as well as during recording sessions, the animals were restrained in a Foringer-type primate chair, located in a sound-attenuated chamber. The behavioral setup is illustrated in Fig. 1. At all other times the animals were kept in their home cages. The only time that animals had access to water was during the behavioral sessions. In training and during recording sessions water was delivered through a spout that was directed to the animal’s mouth.

The acoustic signals were delivered from a speaker mounted 2 m away and directly in front of the animal. Two 6-volt indicator lamps, 22 cm apart, were mounted 25 cm in front of the animal at eye level and were used to present the light stimuli (see Fig. 1). The rise-time of the light stimulus was 5 msec. The animal responded on a spring-loaded lever which used a photoelectric switch to avoid the click artifacts associated with mechanical switch closures.

Initial training consisted of two simple discrimination tasks: Sounds Only and Lights Only (Fig. 2). The first task was to discriminate a 200-msec burst of white noise from a 200-msec tone burst of any frequency. Each monkey was trained to push a bi
directional lever to the right in the presence of a tone and to the left in the presence of noise. Animals were rewarded for a correct response with a 0.1 cc drop of water, while the only punishment for an error was a 5-sec time-out. In the Lights Only condition each monkey was similarly trained to discriminate a 200-msec flash of light coming from the right from a 200-msec flash of light coming from the left by only reinforcing a lever push in the corresponding direction. Responses made earlier than 50 msec after the termination of the stimulus were not rewarded. The average interstimulus interval was 2.5 sec.

In the next stage of training the light and the sound stimuli were combined so that the two different modalities signalled conflicting responses (i.e., Tone + Left Light, Noise + Right Light). In a block of 100 stimuli one modality was 'relevant', meaning that the stimuli in this modality would always indicate the direction in which a lever push would be reinforced. The relevant modality was alternated between blocks of trials so that the animals learned readily to switch from one modality to another. Since the animal could have achieved a perfect score by attending the irrelevant modality and responding in the direction opposite to which it had been trained in conditions I and II, Sounds Only and Lights Only, this condition was used only for training purposes.

In the final conditions stimuli from the two modalities were still presented simultaneously, but the stimuli were paired randomly. The 4 possible stimulus combinations are shown in Fig. 2 under conditions III, Sound Relevant/Light Irrelevant, and IV, Light Relevant/Sound Irrelevant. With these two conditions we could keep the sensory stimuli the same and compare the effects of shifting from one behavioral condition to the other. In 2 of the 4 stimulus-combinations, stimuli from both modalities would signify a response in the same direction. For example, Tone and Right Light was considered a 'Same' combination since the Tone signaled a response to the right and a Right Light also signaled a response to the right. For the other two stimulus combinations, the stimuli would signify opposite responses ('Opposite' combination), for example, Noise (left response) and Right Light (right response).

In a block of 100 trials one modality was chosen to be the relevant modality; the relevant modality alternated between light and sound in blocks of 100 trials. The animal was cued to switch to the relevant modality usually by presenting a block of stimuli in that modality alone (Conditions I or II, Sounds Only or Lights Only). Some animals were also trained to shift between conditions by means of a cue light. Training was considered complete when animals were able to shift between relevant modalities a number of times within one session while performing at a 90% correct level. (The percentage of correct responses was derived from the ratio of correct responses to the sum of correct responses and errors.)

Following completion of training, which averaged 2–3 months/monkey, the animals underwent aseptic surgery during which a restraint lug and two stainless steel chambers were implanted on the monkey’s skulls. The chambers were positioned over the left and right hemispheres so that an electrode advanced through them would enter perpendicular to the superior temporal plane, in which the primary auditory cortex is located. The bone underlying each chamber was removed, leaving the dura intact.

After two days of recovery the monkeys resumed their training with their heads restrained. Five days of retraining were usually sufficient for the monkey’s performance to return to preoperative levels at which time the recording sessions began.

Single-unit recording

For the recording sessions the animals were seated in a primate chair inside a sound-attenuated room with their heads restrained. For each session one of the chambers was filled with a viscous silicone fluid (Dow Corning 360 Medical Fluid) and covered with a Kopf X-Y stage that allowed 10 mm × 10 mm of calibrated movement over the chamber. A glass-coated platinum-iridium microelectrode (typical impedance: 1–4 MΩ) placed in a 22 gauge stainless steel guard tube was inserted into the chamber. The guard tube was advanced until its sharpened point penetrated the dura. The guard tube was then fixed in place and the electrode advanced through it into the brain using an hydraulic microdrive.

The signal from the electrode was first led into a preamplifier with capacitance compensation. The signal was further amplified with a Grass PS1 amplification and passed through a bandpass filter (SKL 302) with the lower and upper cutoff at 180 Hz and 8 kHz, respectively. The filtered signal was monitored by a loudspeaker and an oscilloscope and passed to a special waveform analyzer that classified spikes on the basis of their shapes and amplitudes. In cases of more than one identifiable spike in a record, the experimenter could specify which one of the spikes would be fed to the laboratory computer (Varian 620-I) and displayed on-line in a dot display.

The acoustic stimuli were generated by a programmable waveform generator (Wavetek 154) and a General Radio Co. noise generator (General Radio 1390B). Both stimulus sources were connected through a programmable stimulus selector to an electronic switch with a rise–fall time of 10 msec. Stimulus duration was 200 msec. The electronic switch output was connected through a programmable attenuator and a mixer to an audio amplifier that drove the speaker placed inside the chamber. A continuous noise of 30 dB SPL was introduced into the chamber to mask any extraneous noises. The tone and noise-burst stimuli were approximately 50 dB above masked threshold for a human observer.

All the behavioral equipment, which included the response lever, the indicator lamps and the water reward solenoid, was under computer control. The monkeys were viewed throughout the recording sessions through a closed circuit television system. Each recording session proceeded under a computer program that operated in two modes: a search mode and a behavioral mode. The search mode enabled the experimenter to select a stimulus, attenuation level and interstimulus interval. The stimuli, presented in blocks of 100 trials, could be either noise bursts, tone bursts of one frequency, tone bursts of frequencies changing sequentially or randomly to cover a range of 10 kHz in 0.1 kHz steps, or swept tones over a range of 10 kHz. The search mode was used to find units responsive to acoustic stimuli and to determine the best frequency of units driven by tones. When possible, a frequency capable of exciting a strong response was used as the tone frequency in the behavioral phase of the experiment. The activity of the unit during the search mode was displayed on-line as a dot
display with the time axis beginning 200 msec before the stimulus and covering a period of one second. The interstimulus interval was either 1 or 2 sec. After the desired number of stimuli had been presented (typically 100 trials), the unit data were stored on magnetic tape. In the search mode a visible light in the lever box was turned off, giving the monkey a cue that no reward was available during this time.

In the behavioral mode the computer controlled the presentation of the light and sound stimuli and reinforcement, tallied the behavioral scores and collected and displayed the single-unit data on-line. The unit activity to noise and tone stimuli was separated according to the kind of behavioral response: correct response, error (lever press in the wrong direction) or miss (no response). Accordingly, the on-line and off-line dot displays were organized so that unit activity for each trial was assigned to the particular part of the display that corresponded to the acoustic stimulus and the behavioral response for that trial. For the main conditions III and IV (Sound Relevant and Light Relevant), the correct responses were subdivided according to whether the combined light and sound stimulus was a Same or Opposite combination.

With these displays, information was immediately available on both the animal's behavioral performance and on unit responsiveness for the various stimulus-response combinations. The stimulus, behavioral response, and unit activity for each trial were stored on digital tape for off-line analysis.

Data analysis

In off-line analysis the dot displays for all units were routinely photographed and peristimulus time (PST) histograms were plotted for each behavioral condition. Only trials with correct behavioral responses were used in the comparisons between Light Relevant and Sound Relevant conditions and between Same and Opposite stimulus combinations. The PST histograms covered a period of 1 sec beginning 200 msec before the onset of the stimulus. They were normalized with ordinates scaled in spikes/sec. To aid in comparing a unit's activity in the various behavioral conditions, difference PST histograms were computed by subtracting the PST histograms from each condition from every other condition. The plots for the difference PST histograms also contained the mean difference in firing rate for each of three time periods, a period of stimulus-bound activity plus a pre- and post-stimulus period.

In comparing unit responses for changes in activity between conditions, two independent judges examined the dot displays, PST and difference histograms. In order for a unit to be classified as showing a change in activity, both judges had to agree that a change had occurred. Otherwise the unit was assigned to the 'no change' category.

Histology

Lesions were made at the end of tracks with successful recordings by passing 10 μA for 8 sec. After placing 10–15 tracks in each chamber, the location and orientation of the chambers were marked by inserting 4 stainless steel pins through each chamber. The pins were inserted with the same technique that was used to insert electrodes. They formed a rectangle on the superior temporal plane, outlining the area from which recordings were made. The brains were then perfused with 10% formalin solution, removed and fixed. After fixation, the part of the parietal lobe overlying the superior temporal plane was trimmed away and acrylic brain casts were prepared. The location of the pins and the locations of the electrode tracks were marked on the superior temporal plane of the brain casts. The tissue was embedded in celloidin, sectioned in the sagittal plane in 35 μm steps and stained with cresyl violet. Electrode tracks were assigned to the primary or a secondary field based on lesions or their coordinates referenced to the position of the steel pins.

RESULTS

Behavioral results

The 6 animals trained for this task were very similar in the relative amount of training required for acquisition of each stage of the discrimination. With each successive animal there was a trend for the total amount of required training to decrease, probably resulting from the adoption of more effective shaping techniques during the early stages of the training. Mean number of sessions for the various phases of training were as follows: thirteen 2-h sessions were required to shape the animals to drink from the water tube and push the lever in both directions. After this initial training, condition I, Sounds Only, required 8 sessions and condition II, Lights Only, an additional 5 sessions. To train the animals to perform conditions III and IV, Sound Relevant and Light Relevant, at a 90% correct level involved a further 21 sessions. The animals continued in training for 31 sessions until they could consistently switch between conditions III and IV.

During recording sessions separate scores were computed for conditions III and IV according to the stimulus combination, Same or Opposite. For the Sound Relevant condition the mean score was 93% in Same and 71% in Opposite combinations, for an average score of 83%. For the Light Relevant condition the mean score for Same combinations was 97% and 79% for the Opposite combinations, for an average score of 88%. The slight decrease in performance during recording sessions from the 90% or above level observed during training was possibly related to the increased length of the recording sessions and the frequent interruptions caused by searching for units.

Unit sample

Of the approximately 100 units studied in 6 monkeys, 72 met the following conditions for inclusion in the final sample: (1) recordings from at least two behavioral conditions, (2) behavioral performance during these conditions above the 75% correct level (average of Same and Opposite combination trials) and (3) consistent recordings on repetitions of conditions. For most of the 72 units 4 different behavioral and two search conditions (a total of some 600 stimulus presentations) were available for analysis. The limiting factor for the number of units recorded in a session was the amount of water for which an animal would work in a session. The average amount of 120 cc, at 0.1 cc per reinforcement, permitted 1200 reinforced trials per recording session.
Sixteen of the 72 cortical units were located in the primary auditory field (AI). The remaining units were located adjacent to the primary area in the rostral (8 units), lateral (14 units) or caudal (34 units) areas. No differences in response patterns, spontaneous activity, or latency of response were found between units in the primary area and those in the secondary area. Nor could any differences between these two areas be demonstrated when comparing the two groups of units for changes between the performance–non-performance conditions or between the Light Relevant and Sound Relevant conditions. Thus, units from both areas were pooled for the analyses described in this section.

In one respect, however, units in the primary area could be distinguished from those in secondary areas. All of the 16 units in the primary area responded to tone bursts and of these units 9 responded to both tone bursts and noise bursts. Yet among the 56 secondary area units, 16 responded to noise bursts but not to tone bursts, 16 responded to tone bursts but not to noise bursts, and 24 responded to both tone bursts and noise bursts. For the 33 units responding to both tone and noise bursts the kinds of changes observed in comparing performance vs. non-performance and Light Relevant vs. Sound Relevant conditions were usually the same for both the tone and noise stimuli. Only three units demonstrated opposite changes for tone and noise stimuli.

Units were examined in the Light Only behavioral condition for possible responses to light stimuli. No changes in activity patterns could be detected for the first 300 msec after the onset of the lights. For 6 units weak changes in the activity pattern could be detected at latencies from 300 to 400 msec after the light onset, but since reaction times fell within that interval the possibility that such changes were related to the lever push rather than to the light stimulus could not be excluded. Therefore we have chosen to consider only changes in stimulus-evoked activity that occurred within 300 msec of stimulus onset.

Comparison of unit responses in the performance and non-performance conditions

In the search (non-performing) condition stimuli were presented at a regular rate in order to locate auditory units and to determine their responsiveness to noise and tone bursts. During this condition animals usually sat quietly and made no behavioral responses. Stimuli were usually presented once per second in the search mode. Since there are some adaptation effects at this rate, comparison of the strength of these acoustically evoked responses obtained in the non-performing condition with those obtained in the performing condition is not appropriate. We can say that the patterns of the evoked responses for the same acoustic stimulus were quite similar under both conditions.

For 18 units in two monkeys the search stimuli were presented a rate of 1/2 sec in order to approximate the presentation rate during the behavioral condition. In order for a unit to be categorized as showing a change in responsiveness related to performance vs. non-performance, that change had to be present when comparing each non-performance condition with every performance condition (see Fig. 2). If the evoked response in any of the performance conditions was equivalent to that of the non-performance conditions, then the unit was classified as showing no change. If the last non-performance evoked response did not repeat earlier ones the unit was excluded from the sample. For each unit that responded to both noise bursts and tone bursts, comparisons were made separately for the two stimuli. These were called
Fig. 4. PST histograms for correct responses in condition III, Sound Relevant and IV, Light Relevant for unit 137-4-1L. The acoustic stimulus for all four histograms was identical. Stimulus: noise bursts, 200 msec duration.

'response comparisons'. Twelve response comparisons showed no difference between the performing and non-performing conditions, 6 response comparisons showed greater activity in the performing condition, and seven comparisons showed greater activity in the non-performing condition.

Comparison of unit responses in the Sound Relevant and Light Relevant conditions

As indicated in the Methods section the aim of the behavioral training was to train a monkey to perform at a high level in the Sound Relevant condition for a block of 100 trials (see Fig. 2), then with an appropriate cue to perform at a high level in the Light Relevant condition for a block of 100 trials. We then studied a single unit while alternating a monkey's behavior between the two conditions so that unit responses to identical acoustic stimuli could be compared while a monkey was either attending the sound or the light part of the combined stimulus.

Fig. 5. PST histograms as in Fig. 4 for unit 261-7-1R. Stimulus: 1.4 kHz tone bursts, 200 msec duration.

Figure 3A shows the dot display used for analyzing unit activity obtained online in the Sound Relevant and Light Relevant conditions. The display is divided into quadrants, and each quadrant in turn is divided into an upper and lower part. The left half of the display shows unit activity when the behavioral responses were correct. The right half of the display shows unit activity when the behavioral responses were incorrect. The upper half of the display shows responses to tone bursts, the lower half responses to noise bursts. Unit activity for correct behavioral responses was segregated within a quadrant according to whether the stimulus pattern was a Same or Opposite combination (see Fig. 2, conditions III and IV). Unit responses obtained when behavior was incorrect were segregated according to whether the response was a 'miss' (no lever push) or an 'error' (lever push in the wrong direction). For the dot display illustrated the condition was Light Relevant. It should be noted that in all blocks of trials the four stimulus conditions were presented in a random order, and the unit responses displayed in the appropriate place in the dot display.

The PST histograms in Fig. 3B make evident a number of features of the sound
evoked activity. For the tone burst stimuli these PST histograms illustrate an extreme difference in the amount of evoked activity depending on whether the stimulus combination was Same or Opposite. The tone burst, when presented with a right light (Same) evoked an ‘on’ and ‘off’ excitatory response and a ‘through’ suppression; when presented with a left light (Opposite) the ‘on’ and ‘off’ components were diminished and only the ‘through’ suppression was seen. As with tone bursts, noise burst stimuli for this unit also evoked stronger responses for the Same combinations.

Examples of PST histograms used for the comparison of behavioral conditions and stimulus combinations for three different units are presented in Figs. 4, 5, and 6. In Fig. 4 the acoustic stimuli were noise bursts. In this instance evoked activity was not considered different for the Same and Opposite combinations for either the Sound Relevant or the Light Relevant conditions. Spontaneous activity of this unit did gradually increase during recording, as is evident in the Light Relevant histograms which are for activity recorded 20 min after the Sound Relevant histograms; however, evoked unit activity remained quite stable. It is obvious that the responses in the Light

Fig. 6. PST histograms as in Fig. 4 for unit 261-12-2R. Stimulus: 2.6 kHz tone bursts, 200 msec duration.

Relevant condition were relatively strong while those in the Sound Relevant condition were weak. In Fig. 5, PST histograms for tone bursts from another unit show virtually no response in the Light Relevant condition and clear, short-latency on-responses in the Sound Relevant condition. Here the response for the Opposite stimulus combination was greater than the response for the Same combination in the Sound Relevant condition. This is in contrast to most units which showed stronger responses for the Same than for the Opposite combination.

In Fig. 6 responses of another unit to tone bursts are illustrated. The short-latency on-responses to the Opposite combinations were stronger in the Sound Relevant condition than in the Light Relevant condition. In fact, for the Opposite combination there was virtually no on-response for the Light Relevant condition. Comparing Same and Opposite responses, we find them greatly different in the Light Relevant condition, but not significantly different in the Sound Relevant condition.

The results of such comparisons for all well-studied units are summarized in Figs. 7 and 8. Since there was no obvious difference in these comparisons for units in the primary field and those in the surrounding auditory cortical fields, the results for units from all locations are pooled. Results are given in terms of ‘response comparisons’. If a unit responded to both tone bursts and noise bursts there could be 4 entries from that unit in the histogram of Fig. 7 (responses to the Same combination and to the Opposite combination for tone bursts and for noise bursts), and 4 entries in the histogram for Fig. 8 (responses in the Sound Relevant and in the Light Relevant condition for tone bursts and for noise bursts). A unit which responded only to tone bursts or noise bursts could have only two entries in the histogram. Some units were studied in either the Sound Relevant condition or the Light Relevant condition, but not both. For these units there could be comparisons for the histogram of Fig. 8 but not for the histogram of Fig. 7 (accounting for the
Fig. 8. Comparison of strengths of evoked unit activity in the Same and Opposite stimulus combinations. S > O, S = O, and S < O indicate greater, equal, and less responsiveness, respectively, for the Same stimulus combination as compared to the Opposite stimulus combination. Response comparisons for noise and tone and response comparisons for Sound Relevant and Light Relevant conditions are combined in the histogram.

greater number of response comparisons in Fig. 8). Chi-square tests of the separate distributions that were pooled to produce the histograms in Figs. 7 and 8 revealed no significant difference (P > 0.05) among the separate distributions.

Fig. 7 indicates that in comparing unit responses for the Sound Relevant and Light Relevant conditions 66% of the comparisons (51/77) were different depending on which cue — sound or light — was relevant. The number of comparisons with stronger responses for the Sound Relevant condition (26) was nearly equivalent to the number with stronger responses for the Light Relevant condition (25). Of the 77 comparisons, 26 showed no differences between Sound Relevant and Light Relevant conditions. For a given unit the Same and Opposite stimulus combination usually produced similar changes; only two units showed a stronger response in the Sound Relevant condition for the Same combination, while in the Light Relevant condition these units had a stronger response for the Opposite combination.

Fig. 8 shows that the Same combination was far more likely to evoke a stronger response than the Opposite combination. This result was observed regardless of which modality was the relevant cue. Fifty-two out of 108 unit comparisons (48%) had a stronger response for the Same combination while only 9 (8%) had stronger responses for the Opposite combination. Forty-seven comparisons (44%) showed no differences between the Same and Opposite combinations.

DISCUSSION

Comparisons of unit activity in performing and non-performing conditions

As has been reported previously by Miller, requiring the animal to perform a behavioral task did increase the sound evoked activity of some units in the auditory cortex. However, unlike those results, some of the units in the present study that did change showed a decrease in stimulus-elicited activity when the animal was performing. Also, about as many comparisons showed no change between performance and non-performance conditions as showed a change. These differences between the present results and those of Miller may be due to a number of factors, such as the definition of a criterion for judging whether a change occurred, and the type and amount of behavioral training required of the animal.

It is interesting to note that the performance-related changes in unit activity occurred at relatively brief latencies. If a unit showed differences in responsiveness, those differences would usually be apparent within 50 msec of stimulus onset. These changes in unit activity contrast with the changes in the scalp-recorded auditory evoked potential in humans where task- or attention-related changes are not seen earlier than the N1 component of 80–100 msec. It is unlikely that the middle-ear sound evoked reflex could account for the early latency effects since the stimuli were probably below the threshold for activation. Even if present at the sound intensities used here the latency of the reflex would be expected to be longer than the latency of the observed changes in unit activity. Moreover, since the Same and Opposite trials were interleaved in time and still showed consistent differences, a peripheral mechanism would require the unlikely possibility that middle-ear contractions would be elicited only for certain light/sound stimulus combinations. Other studies employing attention paradigms have also showed that peripheral mechanisms are not a likely cause for attention-related effects observed at the cortex.

Nor is it likely that when it occurred, the altered unit activity for correct behavioral trials was due solely to the fact that only the correct trials were reinforced. To investigate the relationship between alterations in evoked activity and reinforcement we examined separately those behavioral trials where the animal did not respond and was not reinforced (misses). Although only a few blocks of trials had a sufficient number of misses for analysis, for 12 out of 14 blocks the units' activity for misses was similar to that for correct, reinforced trials rather than to activity from the non-performing condition. This indicates that on a particular trial a behavioral response or reinforcement does not have to follow the stimulus in order for unit activity to be affected. Because the misses were mixed with correct, reinforced trials, it is possible that the reinforcement of correct responses is sufficient to alter evoked activity for all stimulus presentations in a given block of trials. Furthermore, it should be noted that the changes in unit activity which we analyzed occurred more than 250 msec prior to responses or delivery of reinforcement.

Comparisons in the Sound Relevant and Light Relevant conditions

Our principal finding was that about two-thirds of the unit comparisons did show that neural activity in the auditory cortex was affected by alternating between the Sound Relevant and Light Relevant conditions. Moreover, the number of comparisons with stronger responses in the Light Relevant condition was just about equal to the number with stronger responses in the Sound Relevant condition. Thus, our results indicate that while selective attention can have an effect on auditory corti-
cal neurons, the effect is not limited to conditions where the auditory modality is the relevant cue. We find it surprising that the Light Relevant condition should have had such a potent effect on auditory cortical neurons, especially since light stimuli alone did not evoke responses in the post-stimulus period we analyzed (0–300 msec). Since the changes occurred at latencies as early as 15–20 msec, which is earlier than the initial latency of unit discharge (35–70 msec) in the cat visual cortex to flash stimuli, it is unlikely that the initial interaction between auditory and visual modalities occurred at the cortical level. The lack of direct anatomical pathways between the auditory and visual cortices also makes a cortical site of interaction unlikely.

The other salient result concerning changes in neural activity during behavior is illustrated in Fig. 8. More than half the unit comparisons showed that Same and Opposite stimulus combinations evoked responses of unequal strength. In 85% of those comparisons judged unequal the Same combination evoked the stronger response. For these comparisons, unlike the Sound Relevant vs. Light Relevant comparisons, the evoked unit responses to Same and Opposite stimulus combinations were randomly interleaved in a block of 100 trials. Thus the changes could not be due to any slow variations in responsiveness of the auditory cortex.

An untrained monkey with no previous experience with the stimuli of the present experiment was used to test for the possibility that some response artifact made the acoustic stimuli unequal in the Same and Opposite combinations. Chambers for recording were implanted, and in experimental sessions the head was restrained and recordings were made just as for the other monkeys. The animal received no reinforcement and did not manipulate the lever. For each unit recorded the monkey was presented with a block of 100 stimulus presentations of Same and Opposite light and sound combinations randomly interleaved as in the Sound Relevant and Light Relevant conditions. For all 28 units studied, response strengths to Same and Opposite combinations were equal.

The training procedure of the present experiments was designed to lead the animals to use selective attention in the Sound Relevant and Light Relevant conditions. The fact that the Opposite stimulus combination did result in much lower scores (71% and 79% for Sound Relevant and Light Relevant conditions, respectively) than the Same combination (95% and 97%), indicates that selection of the monkeys were not able to completely ignore the irrelevant part of the combined stimulus.

We have considered other strategies the monkeys may have used. One possibility is that they did use selective attention, but their attention would occasionally shift to the irrelevant modality. Such lapses would be rewarded under Same stimulus combinations but would result in errors for Opposite combinations. This possibility is in keeping with the obtained behavioral results. An alternative strategy would be for the monkeys to attend both modalities and associate the correct behavioral response with each of the 4 stimulus combinations for a given Sound Relevant or Light Relevant condition. Reference to Fig. 2 shows that the Same stimulus combinations would indicate the same direction of lever press in both behavioral conditions, Sound Relevant and Light Relevant, while the Opposite stimulus combinations indicate opposite directions of lever press for the two conditions. Thus, it would be easier to learn to respond correctly to the Same stimulus combinations, which also fits the behavioral results. However, an animal would have to reverse these stimulus-response associations during blocks of cuing trials. It thus seems unlikely that monkeys would use a strategy so complex and dependent on memory, and that all of the efforts to push them toward using selective attention would fail so completely.

In order to determine how humans would solve the task we studied 6 human subjects. Two subjects were college sophomores. The other 4 were school children of ages 9–14. The subjects were told only that the lever was to be pushed left or right, and that they would be paid according to the difference in score on two visual counters (one of which counted correct responses, the other errors). The subjects were given the same sequence of conditions that the monkeys received in training. After 5 days completed the training sequence with performance at virtually the 100% correct level within two half-hour sessions. When the trained human subjects made errors, it would be on the initial trial. Performance was usually error-free for the remainder of that condition. In contrast, the monkeys, even when well trained, would have a few errors distributed throughout a block of trials. Interviews with the human subjects revealed that they all attended one modality and ignored the other when performing the task, which, a priori, does seem to be the simplest solution.

For trained animals the single unit data show, on the average, that strong sound-evoked response occurred for the Same than for the Opposite stimulus combinations. These neural results correlate with the behavioral results, which showed higher average correct score for the Same than for the Opposite combinations. We might thus speculate that, in general, strength of unit responsiveness is correlated with frequency of reinforcement, since higher scores would produce more frequent reinforcement. We examined this possibility by comparing unit responsiveness in those cases where the same behavioral condition was repeated for a unit, and the behavior score for the repeated condition differed from the original score. In these cases changes in response strength were correlated with changes in behavioral scores (i.e., frequency of reinforcement).

Thus the differences in response strength between the Same and Opposite combinations were not simply related to the frequency of reinforcement within the short time period of recording from a single unit. Nevertheless, for all 6 trained animals, not for the naive animal, unit activity was generally greater for the Same stimulus combination, which suggests that it was the months of behavioral training which modified neural responsiveness in the auditory cortex to a particular sensory stimulus. In fact, changes in inferior colliculus and medial geniculate unit activity during behavioral tests have been reported. The mechanism of such modification of cortical responsiveness merits further study.

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