

# Concurrent measurement of the detectability of tone bursts and their effect on the excitability of the human blink reflex using a probe-signal method

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## Abstract

The probe-signal method has shown that auditory signals that are either presented more often in a series of trials or that are immediately preceded by cues of the same frequency on a single trial are detected more readily than signals of other frequencies. The frequency range in which detection is favored defines an attentional band, which is thought to result from an effective attenuation of deviant frequencies in the cochlea, possibly by activation of the olivocochlear bundle. In a 2IFC procedure in which the first observation interval was preceded by a 1300-Hz cue, subjects detected cued probe tones (at 1300 Hz) but not uncued probe tones (at 1000 Hz or 1600 Hz) at better than chance levels. Concurrent elicitation of a blink reflex by presentation of an air puff in the first observation interval on a random half of the trials showed that cued probes, but not uncued probes, inhibited the size of the blink reflex. These data show that uncued probes do not enter into the low-level sensory processing in the brainstem which is responsible for reflex modification. This finding is consistent with the view that stimuli whose frequency falls outside an attentional band are excluded at the auditory periphery.

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## 1. Introduction

Listeners' ability to detect stimuli with particular acoustic features is determined in part by their recent exposure to stimuli that share those features. One example of this general phenomenon is illustrated by the probe-signal method: brief low-intensity auditory signals in noise are detected when signals of that frequency

occur frequently or when they are preceded by audible cues at the same frequency, whereas probes at other, deviant, frequencies are detected less often or not at all (Greenberg and Larkin, 1968; Macmillan and Schwartz, 1975; Scharf et al., 1987). Systematic variation of probe frequency in this method has revealed an auditory filter centered on the 'expected' probe frequency acquired by repeated presentation of probes at that frequency or by an explicit frequency cue. The filter, which resembles the normal peripheral auditory filter (Patterson, 1974), is sharply tuned with a bandwidth close to that of a critical band, and with an effective attenuation of about 7 dB (Dai et al., 1991). Probes at or near the center frequency of the filter are detected whereas probes whose frequency lies outside the filter

*Abbreviations:* 2IFC, two-interval forced choice; CI, confidence interval; dB, decibel; EMG, electromyographic; Hz, Hertz; N, sample size; OCB, olivocochlear bundle; PPI, prepulse inhibition; SPL, sound pressure level

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band are detected at chance or near-chance levels. The operation of this filter has been characterized by Scharf as an attentional band, and considered to be an elementary form of selective auditory attention that favors the detection of some acoustic events at the expense of others (Scharf, 1998). Other studies have used the probe-signal method to demonstrate the existence of attentional bands for a variety of auditory features, implying that this form of feature selection is a general process in hearing (Arbogast and Kidd, 2000; Greenberg and Larkin, 1968; Wright and Dai, 1994, 1998).

Observations of patients who have undergone vestibular neurectomy to relieve symptoms of Ménière's disease have shown that the surgical procedure has only minor effects on auditory performance in general but specifically reduces frequency selectivity in the probe-signal method. The filter function in the operated ear is flattened or eliminated compared to the same ear before surgery and to the healthy ear after surgery, such that 'unexpected' probe frequencies are detected with high levels of accuracy (Scharf et al., 1994, 1997). This finding implies that the attentional filter operates at the periphery of the auditory system to exclude sounds with deviant frequencies from central auditory processing and is established and maintained by activity of the olivocochlear bundle (OCB), a bundle of auditory efferents which is sectioned by vestibular neurectomy. We report here evidence that sounds with attended, but not unattended, frequencies modify the expression of the blink reflex in normal listeners, indicating that sounds with unattended frequencies do not engage an early stage of sensory processing in the brainstem.

The amplitude of simple brainstem reflexes in humans and other animals is sensitive to low-intensity acoustic events that occur just prior to reflex elicitation (Hoffman and Ison, 1980; Ison and Hoffman, 1983). In particular, brief and insignificant auditory stimuli that appear from about 50–250 ms before elicitation of a blink reflex inhibit the size of the reflex, an effect now commonly known as prepulse inhibition (PPI, Ison and Hammond, 1971, p. 450). Several lines of evidence point to the conclusion that PPI results from a very early and obligatory stage of sensory processing: first, PPI occurs on the first presentation of the prepulse and persists despite repeated presentation of the prepulse alone (Ison et al., 1973); second, it is present during sleep (Silverstein et al., 1980); third, it is present in brain-damaged animals including rats with large cortical lesions (Hammond, 1974) and decorticate rats (Davis and Gendelman, 1977); and fourth, it follows the same general parametric functions in a variety of animals, including frogs, rats, pigeons, rabbits, and humans (Hoffman and Ison, 1992). There is accumulating evidence that auditory prepulses evoke PPI through activation of a circuit within the midbrain that originates in the cochlear nucleus and projects in turn to the inferior colliculus,

the superior colliculus, and the pedunclopontine tegmental nucleus, which makes inhibitory connections with the output motoneurons of the blink reflex in the facial nucleus (Koch and Schnitzler, 1997; Koch, 1999).

Three features of PPI make it a valuable complement to psychophysical measures of sensory function. First, it is an implicit sensory process that does not require conscious decision or response, and hence may be used as an objective indicator of sensory function; second, it reveals the operation of low-level brainstem processing that acts to regulate motor excitability; and third, it is present with prepulse intensities around the psychophysical detection threshold, and hence is a sensitive indicator of sensory function. These three features of PPI were exploited in the present experiment, whose aim was to determine whether probes that fell either within or outside an attentional frequency band would be equally able to inhibit a blink reflex elicited just after their presentation. From previous research, we expected that low-level probes that fall within an attentional band would inhibit the blink reflex (Hoffman and Wible, 1970; Reiter and Ison, 1977). In contrast, if probes that fall outside an attentional band are excluded at the ear and are not processed in the brainstem, as implied by a current view of attentional bands (Scharf et al., 1994, 1997), they would not affect the blink reflex.

## 2. Materials and methods

### 2.1. Subjects

Twenty volunteers (6 males, 14 females) were tested. Their ages ranged from 19 to 29 years with a median of 21.5 years. Four subjects had previously served in a pilot experiment. The Human Research Ethics Committee at The University of Western Australia approved the procedures and all subjects gave informed consent before participating.

### 2.2. Apparatus and general procedure

Psychophysical and reflex indicators of sensory detection were measured concurrently with subjects sitting comfortably in a sound-attenuated room. Acoustic stimuli were generated on a SoundBlaster Live! sound card and presented diotically through Sennheiser Linear HD265 headphones. The acoustic stimuli were calibrated using a Brüel and Kjær artificial ear coupled with a Brüel and Kjær sound-pressure-level meter.

#### 2.2.1. Psychophysical measurement

Immediately before testing, individual auditory thresholds for detecting a 250-ms 1300-Hz tone in diotic broadband noise (overall level 60 dB SPL) were obtained using an adaptive two-interval forced-choice

(2IFC) procedure in which signal level was decreased following two successive correct responses and increased following an incorrect response. This “two-down, one-up” rule estimates the 70.7% correct point on the psychometric function (Levitt, 1971). The initial stimulus intensity was decremented in 5-dB steps until the first error, after which the intensity changed in 1-dB increments and decrements. Ninety stimuli were presented and the threshold was taken as the mean intensity of the last 15 reversals.

In the testing session, psychophysical detection of cued and uncued probes was also measured with a 2IFC procedure. A trial began with a 250-ms 1300-Hz cue which was followed after a 1000-ms interstimulus interval by two successive 250-ms observation intervals separated by a 300-ms interval. The two intervals were indicated by a 250-ms presentation of the numeral ‘1’ or ‘2’ which appeared on the computer screen after each interval. A 250-ms probe tone was presented randomly in either the first or second observation interval. The probe tone was either cued (at 1300 Hz) or uncued (at either 1000 Hz or 1600 Hz), with half the subjects tested with the low-frequency uncued probe and the other half tested with the high-frequency uncued probe. Previous work with the probe-signal method has shown that these frequencies would not be detected differently without cueing. The subjects’ task was to indicate whether the probe occurred in the first or second observation interval by pressing the appropriate response button on a hand-held response box within 2000 ms of the onset of a ‘respond now’ message that appeared on the screen at the end of the second observation interval. Diotic broadband noise with an overall level of 60 dB SPL was present throughout testing. The energy spectrum of the noise was flat (within  $\pm 1$  dB) between 800 Hz and 2 kHz. The spectrum level over this band was 29 dB SPL. The cue and probe stimuli were set at 10 dB and at 3 dB, respectively, above each subject’s detection threshold established immediately before testing. The intensity of the low-frequency uncued probe was decreased by 0.6 dB and the intensity of the high-frequency uncued probe was increased by 0.6 dB to adjust for the shift in masked threshold with frequency (Greenberg and Larkin, 1968). The cue and probe stimuli were gated on and off over 30 ms with a cosine ramp.

### 2.2.2. Blink reflex methods

The corneal blink reflex was elicited by a brief (20 ms) air puff directed to the right eye through a soft rubber nozzle (3-mm diameter). The air pressure required for reliable blink elicitation was obtained for each subject by increasing the source pressure of the air puff in approximately 5-kPa steps until a blink reflex was present on three successive puffs. Air puffs were presented only in the first observation interval and appeared on a random half of the trials. On trials when it was pre-

sented, the onset of the air puff was 188 ms after the onset of the first observation interval. (The indicators of the observation intervals appeared at the end of each interval, rather than throughout the interval, to avoid any stimulus other than a probe from appearing immediately before the blink-eliciting stimulus.) Blink reflexes were thus elicited in each of three experimental conditions: first, trials in which the probe (either cued or uncued) was presented in the second observation interval; second, trials in which a cued probe was presented in the first observation interval; and third, trials in which an uncued probe was presented in the first observation interval. The first of these conditions gives a control measure of blink amplitude in the absence of immediately prior stimulation (the effects of the cue on blink amplitude would decay in the interval of more than 1 s that elapsed from the offset of the cue to the air puff) whereas the second and third conditions give measures of the size of the blink reflex when evoked shortly after the onset of a cued and uncued probe respectively. The 188-ms interval from the onset of the first observation interval (and hence from the onset of a first-interval probe) to the air puff was selected to be in the optimal range of interstimulus intervals for producing PPI. The electromyographic (EMG) activity of the blink reflex was measured with two 6-mm diameter gold-plated electrodes placed on the lower eyelid over the orbicularis oculi muscle and on the lateral canthus, and a third electrode on the mastoid process as ground. The EMG was amplified (with half-amplitude cut-off frequencies of 10 and 1000 Hz), digitized at 4000 Hz with 12-bit analog-to-digital conversion, and stored for later manual scoring of the area of each blink (in mV ms).

Trials were presented in blocks of 14, which were made up of 10 trials in which a cued probe appeared randomly in either the first or second observation interval and four trials in which an uncued probe appeared randomly in one or other of the intervals. The presentation order of cued and uncued probes within each block was random subject to the constraint that the required number of each probe type was presented. Twenty trial blocks were given for a total of 280 trials, 200 of which contained a cued probe in either the first or second interval and 80 of which contained an uncued probe in either the first or second interval.

### 2.3. Data analysis

Psychophysical performance was quantified as the proportion of cued and uncued probes detected correctly and as the median time taken (in ms) from the end of the second observation interval to signal the psychophysical response. The accuracy scores were subject to arcsin transforms before analysis, and the resultant values back-transformed for presentation. Median blink amplitudes in the conditions in which a cued or uncued

probe appeared in the first observation interval (and which hence preceded the air puff by 188 ms) were expressed as ratios of the median blink amplitude in the condition in which the probe appeared in the second observation interval, and which hence gave control reflex amplitudes in the absence of immediately prior stimulation. Amplitude ratios near one indicate that the probe had little or no effect on the blink reflex whereas amplitude ratios less than one indicate the presence of PPI. The amplitude ratios were log-transformed before analysis and back-transformed values are presented (the mean values reported are therefore the geometric means of the untransformed ratios). The 95% confidence intervals (CIs) around mean values are reported.

### 3. Results

#### 3.1. Psychophysical data

All subjects detected cued probes more frequently than uncued probes. The mean proportion correct was 0.75 (95% CI = 0.67, 0.83) for cued probes and 0.51 (95% CI = 0.47, 0.55) for uncued probes. The mean proportion of correct detection was similar and at chance for both uncued probe frequencies (0.51, 95% CI = 0.49, 0.53; and 0.48, 95% CI = 0.42, 0.55 for the 1000 and 1600 Hz probes, respectively). Detection of cued probes was slightly poorer on trials on which an air puff was presented. The mean proportion correct was 0.71 (SE = 0.04) and 0.75 (SE = 0.04) for trials with and without an air puff, respectively. Median response time was briefer for cued than uncued probes for 17 of the 20 subjects. The mean of the median response times was 378 ms (SE = 32) for cued probes and 441 ms (SE = 34) for uncued probes; the difference between these two means was 63 ms (95% CI = 34, 92). The two psychophysical performance measures, the proportion of cued probes detected correctly and the difference in response times for cued and uncued probes, were correlated ( $r = 0.60$ , 95% CI = 0.22, 0.83).

Analysis of the blink reflex was restricted to 19 (of 20) subjects whose psychophysical performance showed clear evidence of an attentional band. This was done by constructing 95% confidence intervals around each subject's proportion of correct detections of both cued and uncued probes, and selecting only those subjects whose lower confidence limit for detection of cued probes was greater than the chance level of 0.5 (and hence indicated better than chance detection) and whose lower confidence limit for detection of uncued probes was less than 0.5 (and hence indicated chance level performance). These criteria led to the exclusion of one subject (whose lower confidence limit for detection of uncued probes was greater than 0.5, indicating that this subject may have detected these probes above chance le-

vel. The mean proportion of correct detections and the mean median response times for cued and uncued probes for the remaining 19 subjects are shown in the top and middle panels of Fig. 1.

#### 3.2. Blink reflex data

Analysis of blink amplitude ratios in the selected 19 subjects showed clear evidence of PPI to the cued probes but not to the uncued probes (bottom panel, Fig. 1). Blink amplitude ratios were less than one for the cued probes (indicating PPI) in 17 of the 19 subjects, but in only 7 of the 19 subjects for the uncued probes. The

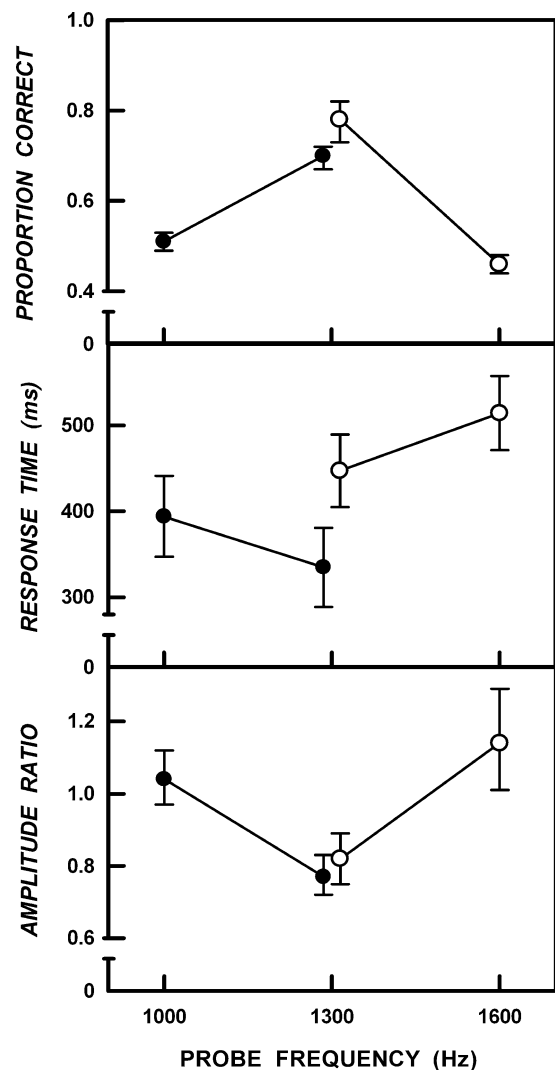


Fig. 1. Performance as a function of probe frequency separately for the subgroups which received the 1000 Hz ( $N = 10$ ) and 1600 Hz ( $N = 9$ ) uncued probe frequencies. Top panel: the mean proportions of probes reported correctly; Middle panel: the mean median response times (in ms); Bottom panel: the geometric mean blink amplitude ratios. The symbols depicting performance at the cued probe frequency (1300 Hz) are offset slightly for clarity. The error bars show  $\pm 1$  standard error of the mean.

mean blink amplitude ratios were 0.81 (95% CI = 0.72, 0.90) and 1.10 (95% CI = 0.96, 1.27) for the cued and the uncued probes, respectively. Cued probes that occurred in the first interval that were correctly reported (and hence likely to have been detected) had an inhibitory effect on the blink reflex (mean amplitude ratio = 0.71, 95% CI = 0.52, 0.96) whereas those that were not correctly reported did not (mean amplitude ratio = 1.20, 95% CI = 0.91, 1.58). This difference was not present for uncued tones that occurred in the first observation interval; these probes did not have an inhibitory effect on the blink reflex whether correctly reported (mean amplitude ratio = 1.11, 95% CI = 0.88, 1.41) or not (mean amplitude ratio = 0.81, 95% CI = 0.52, 1.24).

#### 4. Discussion

The procedure of the current experiment, where a 1300-Hz cue was presented on each trial and where cued 1300-Hz probes were presented more frequently than the uncued probes at either 1000 Hz or 1600 Hz (71% of all probes were at 1300 Hz), established attentional bands in almost all subjects such that the cued probes were detected at better than chance level whereas uncued probes were not detected. These results are in keeping with previous demonstrations using the probe-signal method (see Scharf, 1998). This differential detection of cued and uncued probes in noise was mirrored in the response times, which showed that the psychophysical response to cued probes was made more rapidly than that to the uncued probes. In his review of the psychophysical literature on auditory attention, Scharf (1998) noted that no study published to that time had reported any attentional effect on reaction time, and reported a previously unpublished probe-signal study in which responses to the cued frequency were no faster than those to any of six uncued frequencies. Since the period covered by Scharf's review, one study using a single-interval yes-no procedure in which subjects were instructed to signal their response as quickly as possible showed that detection response speeds decreased systematically with deviation of the probe frequency from the centre frequency of the attentional band, and so followed a similar function to that which described response accuracy (Ison et al., 2002). The two-interval procedure used in the present experiment does not allow exact measurement of detection speed (subjects waited until the end of the second observation interval before signaling their response to a probe heard in the first interval), and subjects were not instructed to respond as quickly as possible. Nevertheless, responses to the cued probes were signaled more rapidly than those to the uncued probes. Together, these two studies show that attentional bands govern both the accuracy with which probes are detected and the speed with which the psy-

chophysical judgments are signaled. Response speed in these conditions might reflect the time taken for the sensory decision to be made or the subjects' confidence in the accuracy of their judgments.

The most important feature of the results reported here is the demonstration that cued probes, which were detected at better than chance levels, inhibited the size of the blink reflex, whereas uncued probes, which were not detected above chance level, did not affect the size of the blink reflex. Although eliciting a blink reflex with an air puff in the first of the two observation intervals interfered with probe detection, the effect was minor and did not prevent the emergence of clear attentional bands, allowing concurrent measures of psychophysical detection and blink reflex excitability. The differential effect of the two probes on the size of the blink reflex implies that cued probes have access to the brainstem circuitry that mediates PPI whereas the uncued probes do not. This result fits with the previous demonstrations that the tuning of attentional frequency bands is compromised by vestibular neurotomy and is behavioral evidence from normal observers that stimuli that fall outside an attentional band are excluded from processing at the periphery of the auditory system (Scharf et al., 1994, 1997). The data further strengthen the argument against the 'heard-but-not-heeded' hypothesis (Scharf et al., 1987, p. 219), which proposes that psychophysical attentional bands are artifacts of a subjectively made decision to report only the cued or more frequently occurring probe frequencies and to ignore other probe frequencies as task-irrelevant. In contrast, attentional bands are not artifacts of psychophysical decision making but reflect the processing of sensory input. The finding that uncued probes are not detected above chance level and do not evoke PPI is suggestive evidence that they are excluded from any form of significant central processing, and is consistent with the view that attentional frequency bands are formed by an inhibitory effect of the OCB on the cochlea. The locus of other features of selective listening remains an open question. The evidence that detection can be determined conjointly by signal duration and frequency, such that signals of an expected frequency are detected poorly unless their duration matches that of a frequently presented (and hence expected) signal, led to the conjecture that detection is based on a time-frequency window whose parameters are determined by the temporal and spectral features of expected sounds (Wright and Dai, 1994; Dai and Wright, 1995). These authors suggested that such a composite window might be formed in part by the activity of duration-selective neurons which have been identified in the auditory midbrain in amphibians and bats (see Faure et al., 2003, for a recent discussion). In this context, it would be of interest to determine whether PPI is evoked by sounds with a cued duration but not by sounds whose duration is uncued. Such a

finding would indicate that the integration of temporal and spectral features of sound, which influences detection, also engages the midbrain circuit responsible for PPI.

Despite the widespread presence of the OCB in mammalian species, little is known of its function in hearing in normal listeners. Detailed observations of human patients treated for the symptoms of Ménière's disease have shown that section of the OCB has relatively minor effects on auditory performance other than selective attention (Scharf et al., 1994, 1997; Giraud et al., 1997; Zeng et al., 2000). The degree of effective attenuation present in an attentional band – about 7 dB – is small, and although significant when dealing with near-threshold events, seems unlikely to have a major effect in listening in a normal acoustic environment (Dai et al., 1991). The OCB has been hypothesized to have an important developmental function in tuning peripheral frequency responsivity to frequently encountered sounds (Scharf et al., 1997; Walsh et al., 1998). It is now clear that the tonotopic organization of the mature auditory cortex is not fixed but plastic, and is capable of rapid experience-triggered reorganization (Weinberger, 1993; Kilgard and Merzenich, 1998; Irvine et al., 2001; Fritz et al., 2003). It is possible, therefore, that the relatively small peripheral effects on frequency selectivity evident in an attentional band are prolonged or even amplified by experience-dependent changes in cortical frequency representation. Selective input of commonly experienced frequencies might increase the cortical representation of those frequencies at the expense of frequencies that are less commonly experienced. Such a change might smooth transient OCB-mediated peripheral changes and, potentially, through descending control of the OCB, amplify the peripheral changes in frequency selectivity. A control system that operated in this way, where peripheral changes evoked central changes that in turn prolonged and amplified the peripheral changes, would give a temporally graded and powerful adaptation of auditory sensitivity to the acoustic environment.

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