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Journal

Psychological Science, 26(7)

ISSN

0956-7976

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Publication Date

2015-07-01

DOI

10.1177/0956797615576533

Peer reviewed



Published in final edited form as:

Psychol Sci. 2015 July ; 26(7): 1006–1013. doi:10.1177/0956797615576533.

The Rhythm of Perception: Acoustic Rhythmic Entrainment Induces Subsequent Perceptual Oscillation

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Abstract

Acoustic rhythms are pervasive in speech, music, and environmental sounds. Evidence for neural codes representing periodic information has recently emerged, which seem a likely neural basis for the ability to detect rhythm and rhythmic information has been found to modulate auditory system excitability, providing a potential mechanism for parsing the acoustic stream. Here we explore the effects of a previous rhythmic stimulus on subsequent auditory perception. We found that a low-frequency (3 Hz) amplitude modulated signal induces a subsequent oscillation of perceptual detectability of a brief non-periodic acoustic stimulus (1 kHz tone); the frequency but not phase of the *perceptual oscillation* matches the entrained stimulus-driven rhythmic oscillation. This provides evidence that rhythmic contexts have a direct influence on *subsequent* auditory perception of discrete acoustic events. Rhythm coding is likely a fundamental feature of auditory system design that predates the development of explicit human enjoyment of rhythm in music or poetry.

“The perception, if not the enjoyment, of musical cadences and of rhythm is probably common to all animals, and no doubt depends on the common physiological nature of their nervous systems” (Darwin, 1871). This claim, put forward by Charles Darwin in 1871, has recently become a topic of intense interest, both explicitly and unwittingly. Explicitly, research on animals' ability to synchronize their movements to a beat has revealed some success stories, but also more variability than Darwin might have expected (Patel, 2014). More unwittingly, recent demonstrations of the tendency for neural oscillations to entrain to rhythmic features of stimuli (Howard & Poeppel, 2012; Stefanics et al., 2010), for intrinsic neural oscillation and stimulus phase to modulate attention and perception (Henry & Obleser, 2012; Howard & Poeppel, 2010; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Ng, Schroeder, & Kayser, 2012) even beyond the auditory modality (Romei et al., 2008; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008), and for attention to be allocated in oscillatory pulses (de Graaf et al., 2013; Landau & Fries, 2012; Song, Meng, Chen, Zhou, & Luo, 2014; VanRullen, 2013) is consistent with an exceptionally broad neural mechanism for rhythmic entrainment that forms the foundation of sensation across species (Schroeder & Lakatos, 2009), consistent with Darwin's claim.

Although much recent progress has been made in uncovering underlying effects of intrinsic and entrainable neural rhythms in visual perception (citations above), hearing presents an

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different situation in that rhythmic information appears to be coded explicitly as a perceptual feature. Indeed, research in humans and other mammals has provided evidence for the existence of neural codes for representing periodic acoustic information, typically assessed using amplitude modulated (AM) wideband noise signals (Barton, Venezia, Saberi, Hickok, & Brewer, 2012; Baumann et al., 2011; Giraud et al., 2000; Langner, Dinse, & Godde, 2009; Langner, Sams, Heil, & Schulze, 1997). For example, in the cat inferior colliculus, neurons tuned to particular modulation rates have been found (Langner & Schreiner, 1988; Schreiner & Langner, 1988) and in human auditory cortex, modulation rate or “periodicity” maps have been uncovered using functional MRI (Barton et al., 2012). Such findings are consistent with the hypothesis that in addition to spectral filtering accomplished by the cochlea, the auditory system extracts periodicity information computationally (Borst, Langner, & Palm, 2004) and filters acoustic signals into modulation rate channels (T. Dau, B. Kollmeier, & A. Kohlrausch, 1997; Torsten Dau, Birger Kollmeier, & Armin Kohlrausch, 1997).

But what function(s) does rhythmic information serve? Is it simply another acoustic feature allowing the listener to hear the rhythms themselves, for example, the difference between a trot and a gallop or waltz and a samba? Or does rhythmic coding subservise a more fundamental function in hearing? Research involving speech, another stimulus with strong rhythmic features (Pelle & Davis, 2012), suggests the latter by demonstrating that disrupting the natural rhythm of a sentence degrades intelligibility (Ghitza & Greenberg, 2009; Pelle & Davis, 2012) and further that phase information in low-frequency neural oscillations predicts sentence intelligibility (Luo & Poeppel, 2007). It has been argued that the rhythm in speech and other sounds provides a predictive cue to the time of arrival of subsequent critical bits of information (Engel, Fries, & Singer, 2001; Giraud & Poeppel, 2012), a cue that is put to use via stimulus driven entrainment or phase-locking of neural oscillations (or periodicity coding channels) that in turn modulate neuronal excitability for maximal sensitivity during critical time windows (Giraud & Poeppel, 2012; Lakatos et al., 2008; Lakatos et al., 2005). Recent electrophysiological recordings in monkey auditory cortex have shown that entrained oscillatory activity to a train of pure tone beeps persisted even after the stimulation ceased (Lakatos et al., 2013), lending support to the idea that rhythmic contexts could influence subsequent perception. Unfortunately, behavioral correlates of these persisting oscillations were not reported. Some related behavioral work on timing-based attention provides at least *prima facie* suggestive evidence: when the inter-stimulus interval (ISI) of a set of distractor tones predicts the time of presentation of a target tone, pitch judgments are more accurate by up to 10% compared to when ISI does not predict target presentation (Jones, Moynihan, MacKenzie, & Puente, 2002). However, it is unclear whether this sort of temporal attention is due to bottom-up auditory entrainment (our interest here) or from some top-down temporal expectation (Spaak, de Lange, & Jensen, 2014).

The present experiment sought to assess whether a rhythmic acoustic stimulus would induce an *oscillation in perception* that matches the period of the entrained stimulus and persists *for several cycles* even after the driving stimulus stops oscillating. Such an effect has not yet been shown in audition where findings are limited to cases in which an oscillating stimulus persists in the test phase (thus limiting inferences regarding their *predictive* utility) (e.g.,

Henry & Obleser, 2012) or cases where an entrained neural oscillation exhibits post-stimulus persistence with no behavioral correlates presented (Lakatos et al., 2013). A similar effect *has* recently been reported in vision (Spaak et al., 2014) but using a modulation rate (10Hz) that failed to show an effect in hearing (Ilhan & VanRullen, 2012). Given the low-frequency modulation rate of many naturally occurring sounds such as speech, we explored this question at a correspondingly lower modulation rate (3Hz). To reduce temporal prediction effects we avoided a punctate entrainment stimulus and used amplitude modulated (AM) noise instead, which is more similar to the envelope modulation characteristic of natural rhythmic stimuli such as speech. We further reduced temporal prediction effects by using a target stimulus (1 kHz tone) that differed from the entrainment stimulus—unlike Jones et al. (2002) who used tones both as the rhythmic context and the target, thus potentially encouraging perceptual grouping—and by ensuring that the phase of the AM cycle provided no reliable cue to arrival time of the target.

Methods

In a first experiment, five¹ normal hearing adult human listeners were presented on each trial with a wideband Gaussian noise stimulus that lasted 4 seconds. The noise was amplitude modulated at 3 Hz (80% modulation depth) for the first 3 seconds of the stimulus duration (the entrainment phase), then the modulation waveform ended on the cosine phase of the next cycle leaving the final 1 second portion of the noise stimulus unmodulated (Fig. 1). On half of the trials a 1 kHz tone (50 msec duration with a 5 msec rise-decay time) was presented during the unmodulated portion of the noise stimulus at various time points at one of 9 temporal positions. These temporal positions started at the offset of the modulation, and were successively spaced 83.3 msec apart, which is equal to one-quarter of the modulation period. Thus, the 9 temporal positions of the tonal signal covered two full cycles of the expected modulation waveform, had the modulation continued during this period (Fig. 1).

On each trial of a single-interval two-alternative forced-choice task, the subject was required to indicate (via a key press) whether a tonal signal was present during the unmodulated segment of the masking noise. The prior probability of a signal occurring on a given trial was 0.5. When a tone was presented, its temporal position was selected randomly from one of 9 values as shown in Fig. 1, and its level was selected from one of 5 values covering a range of 12 dB to allow measurement of psychometric functions. Each run consisted of 100 trials, and each subject completed a minimum of 20 runs. All procedures were approved by the University of California, Irvine's Institutional Review Board.

Results

Figure 2 shows psychometric functions averaged across 5 subjects for the five signal levels used in our experiment. Trials associated with the second point on the psychometric function (at 6 dB in Fig. 2) were selected for further analysis because this was near the steepest point

¹Sample size was selected as typical for psychophysical studies, which seek to thoroughly characterize the performance of each participant separately using far more trials than is typical for group averaging-type psychological studies. This avoids replicability issues by building in several independent replications (= N-1).

of the psychometric slope (between 0.7 and 0.9), maximizing the likelihood of observing variations in performance.

Figure 3 shows the proportion correct for detecting the tonal signal as a function of temporal position in the unmodulated masking noise. Note that signal-detection performance for all subjects modulates at a rate equal to the masker modulation, and antiphasic to expected modulation, with peak performance occurring near expected dips, and poorest performance associated with expected modulation peaks. Note that signal (tone) level is held constant for the data shown in Fig. 3, but performance varies significantly from approximately 65 to 90 percent (on average). The d' values, as expected, also modulate cyclically by as much as 1.25 units from approximately 1.5 to 2.75 depending on the temporal position of the tone signal relative to the expected modulation phase (Supplemental Fig. 1 [end of present document]).

A single factor repeated-measures ANOVA conducted on the data shown in Fig. 3 revealed a highly significant effect of temporal position, i.e., the modulation phase at which the tone signal was presented ($F_{8,32}=10.61, p<0.001$). Table 1 shows pairwise t-test comparisons across all permutations of temporal positions. The large number of significant results suggests that the significance of the F value is not based on the deviation of detection performance at a single temporal position, but rather results from systematically different detection performances at different phases of the expected modulation waveform.

Top panel of Fig. 4 shows signal-detection performance curves for the 5 subjects superimposed within the same panel, with each curve normalized to a peak of unity. To further analyze the pattern of change in detection as a function of tone temporal position relative to the phase of the expected noise modulation, we calculated the Fourier transforms of these detection curves and found that the peak of the amplitude spectrum for all five curves occurs at 3 Hz which is the frequency of the expected noise modulation. In addition, we examined the phase spectra of these waveforms and found that at the 3-Hz frequency, all five had starting phases near $-\pi/2$ (red line in bottom panel of Fig. 4), the exact opposite phase compared to that associated with the phase of noise modulation ($\pi/2$), suggesting that detection patterns are antiphasic to the noise-modulation pattern. In further support of this finding, we conducted a computational simulation for each observer by scrambling the positions of the detection points of each curve shown in the top panel of Fig. 4 and calculating their Fourier phase spectrum at 3 Hz. Results for a 1000 such random scrambles are shown as open black circles in the bottom panel of Fig. 4. The chance likelihood of all 5 starting phases occurring within 0.5 radians of $-\pi/2$ (gray rectangle) is $2\pi^{-5}$ or $p<0.0005$. Thus our analysis shows, both at the group and individual levels, that signal-detection performance during the non-modulating segment of the noise is modulated at the same frequency but antiphasic to the noise-modulation envelope.

Given that we observed significant modulation in signal detection during the unmodulated part of the masking noise and no evidence that the modulation in performance is declining, in a second experiment we measured signal detection at temporal positions associated with the 3rd and 4th cycles of the expected masker modulation to determine how modulation of performance may decline as a function of time. Three of the five subjects who participated

in the first experiment were available to return and participate in the second experiment. Note that the data in Fig. 3 are associated with the first two expected cycles of masker modulation. Figure 5 shows results of our experiment when the signal to be detected occurred during the third and fourth expected modulation cycles. To facilitate visual comparison, these data are combined with the data for the same three subjects from Fig. 3 (expected cycles 1 and 2). Modulation of performance significantly declines and is less consistent during the 3rd and 4th expected cycles of masker modulation, although one can still observe some residual modulation in performance.

Discussion

Our findings show that a rhythmic acoustic temporal context induces subsequent oscillations in the perception of a non-rhythmic, discrete acoustic event, similar to previous work in the visual domain (de Graaf et al., 2013; Spaak et al., 2014). This effect is substantial in magnitude, resulting in accuracy differences up to approximately 25% and d' fluctuations greater than 1.0 (i.e., more than a standard deviation fluctuation; cf., the $\sim 10\%$ attentional effects reported by Jones et al., 2002).

The anti-phase oscillation of perceptibility argues against a simple attentional, expectation-based explanation of our findings (Spaak et al., 2014), which is a likely explanation for previous auditory studies showing that temporal rhythms can enhance detectability for the *same* stimulus type presented in phase with the rhythm (Arnal, Doelling, & Poeppel, 2014; Jones et al., 2002; Ten Oever, Schroeder, Poeppel, van Atteveldt, & Zion-Golumbic, 2014). In the present experiment, if listeners used the peak of the AM pulses to predict stimulus arrival, one would expect best detection performance at the peak, not the trough, of the expected modulation cycle. This suggests that our experiment tapped into a bottom-up mechanism reflecting the organization of the auditory system itself rather than a top-down attention-driven mechanism reported previously (Jones et al., 2002).

A previous study (Neuling, Rach, Wagner, Wolters, & Herrmann, 2012) reported a *prima facie* similar result to ours using oscillating transcranial direct current stimulation (tDCS) for continuous entrainment (maintained during the detection interval) instead of AM noise that transitioned to unmodulated noise. They reported that the phase of the induced neural oscillation predicted detection performance over a single oscillation cycle, with better detection during the negative half wave of the stimulation cycle. Interpretation of this study is complicated by the fact that tDCS induces discomfort which would oscillate with the stimulation cycle and could therefore indirectly modulate performance as a function of discomfort rather than entrained neural oscillation. In contrast, our study provides a direct demonstration that prior rhythmic entrainment induces a *subsequent* oscillation in perception that persists over *several* duty cycles.

There are at least three possible explanations regarding the source of the presently observed rhythmic entrainment effect. One possibility draws on the idea of nested theta-gamma neural oscillation circuits. The hypothesis is that the slow theta oscillations entrain to the slow stimulus envelope modulation (e.g., as is typical in speech and in our AM stimulus), which in turn modulates gamma activity in local neural networks involved in processing acoustic

features (Giraud & Poeppel, 2012). On one version of this claim, there is an anti-phase relation between theta oscillations and gamma activity (gamma peak=theta trough) (Giraud & Poeppel, 2012). This seems to fit our observations if we assume that the phase relation between our AM stimulus and gamma oscillation is aligned.

Another possible explanation is suggested by considering how the signal-to-noise ratio (SNR) during the detection interval would have varied had the modulation of the entrainment phase continued into the detection interval: SNR would be greatest during the troughs of the modulation, which is where the best signal detection performance was found. Therefore, the effect may be explained as a form of perceptual after effect, an echoic trace of the entrained stimulus. The existence of modulation rate coding in human auditory cortex (Barton et al., 2012) provides a possible neural source for generating such an after effect. This may also explain the recent observation that the power and phase of EEG recorded theta oscillations generated while listening to a mixture of environmental sounds was stronger on target miss trials compared to target hit trials (Ng et al., 2012). This effect was interpreted neurocomputationally as evidence for a “precluding but not ensuring” role for theta oscillations. But if theta power/phase reflects stimulus-driven rhythmic entrainment, as much work suggests (Howard & Poeppel, 2012; Luo & Poeppel, 2007), then the echoic trace of a strongly entrained rhythm may add periodic noise at that frequency to subsequent stimulus presentations leading to an increased detection threshold and more misses on trials that are phase aligned with the entrainment.

We are left with a range of interesting observations: (i) stimulus rhythms entrain neural oscillations and modulate perception, (ii) the phase relation between stimulus rhythms and behavior can vary depending on the task and the stimuli, and (iii) both bottom-up (present experiment) and top-down mechanisms (Jones et al., 2002; Lakatos et al., 2013) appear to be in play. A critical task for future research will be to understand the interaction of these effects and their neural bases. For example, one major question concerns the relation between modulation rate coding (channels or filters) in the auditory system and endogenous neural rhythms, which are found throughout the brain. Both seem to respond to similar stimulus features in the auditory domain but have largely been studied independently. One possibility is that modulation rate coding is a mechanism for bottom-up rhythmic processing of sound whereas endogenous neural rhythms provide a mechanism for attentional selection (Lakatos et al., 2013).

Overall, our findings are broadly consistent with the claim that the rhythm of a stimulus and the rhythm of the brain modulate perception. Whether the effect of rhythmic entrainment in the auditory system reflects a generalized perceptual mechanism or the output of specific channels for coding rhythmic patterns remains an open question. In either case, such mechanisms, likely present in a range of species, could lay the computational groundwork for the development of higher-level uses for rhythmic coding, such as music, thus qualifying Darwin's claim.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

Data are available upon request. This was supported in part by NIH DC03681 and NSF BCS-1329255.

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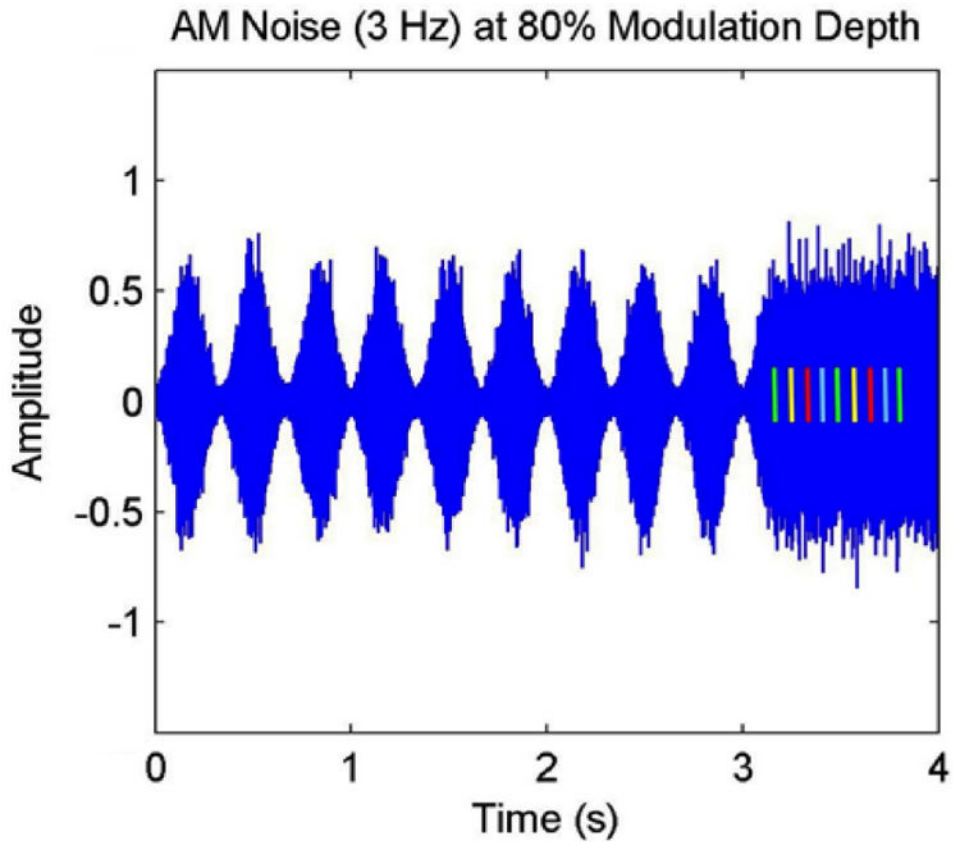


Figure 1.

Stimulus waveform and tone detection time points (colored bars) The green bars represent the 0, 1, and 2 cycle time positions (i.e., peaks of the expected modulating waveform, had it continued). Stimuli were generated using Matlab software (Mathworks) on a Sony Lenovo T400 computer and presented at a rate of 44.1 kHz through 16-bit digital-to-analog converters and Sennheiser headphones (eH 350) in a steel-walled acoustically isolated chamber (Industrial Acoustics Company). The noise stimulus was presented at a nominal level of 70 dB (A weighted).

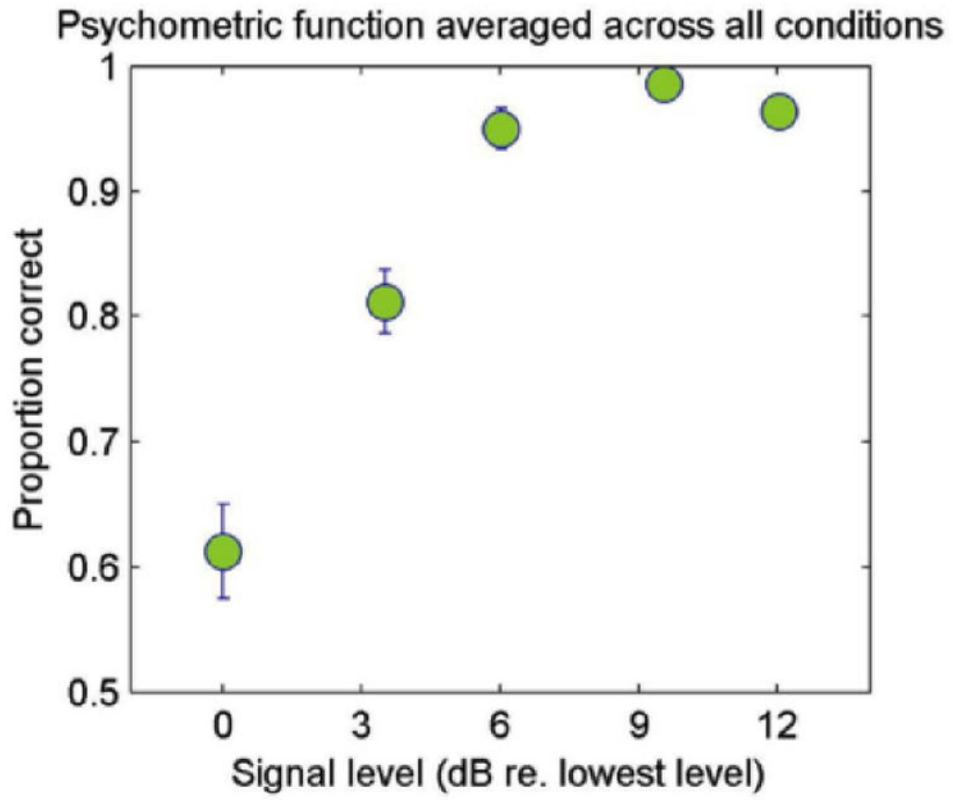


Figure 2. Tone detection psychometric function averaged across five listeners and all conditions. Error bars are ± 1 standard error.

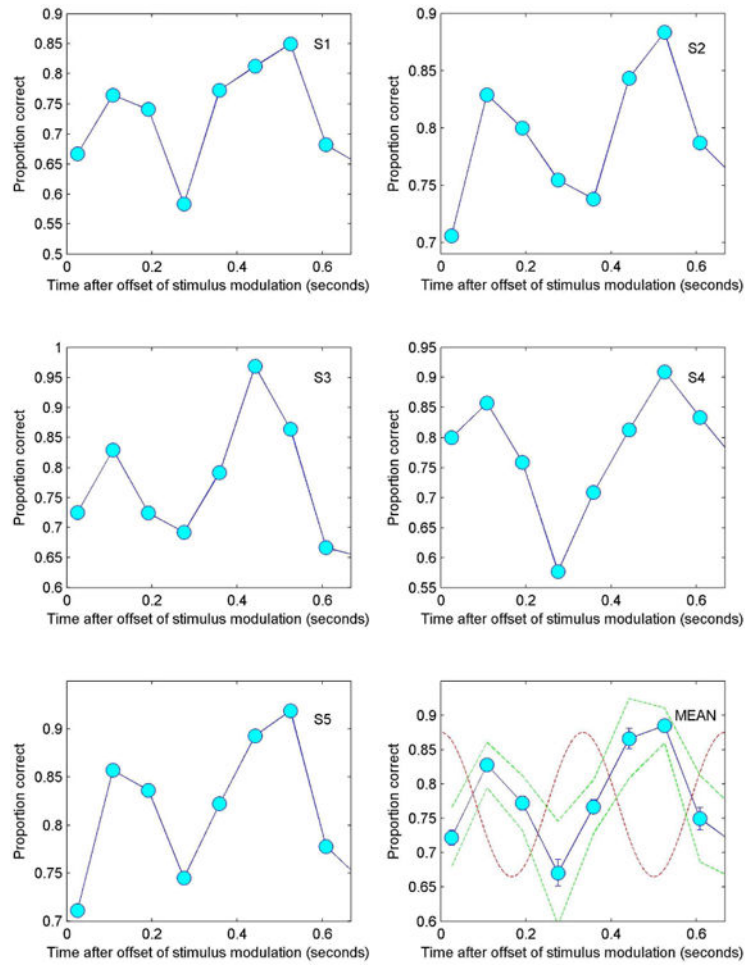


Figure 3. Tone detectability as a function of time after offset of noise modulation. The abscissa represents time after offset of masker modulation (at its cosine phase). Each panel displays data from one subject, with the bottom-right panel showing mean performance. The red dashed curve in the bottom-right panel shows expected masker modulation, had it continued. Green lines represent 95% confidence limits. Error bars represent 1 standard error.

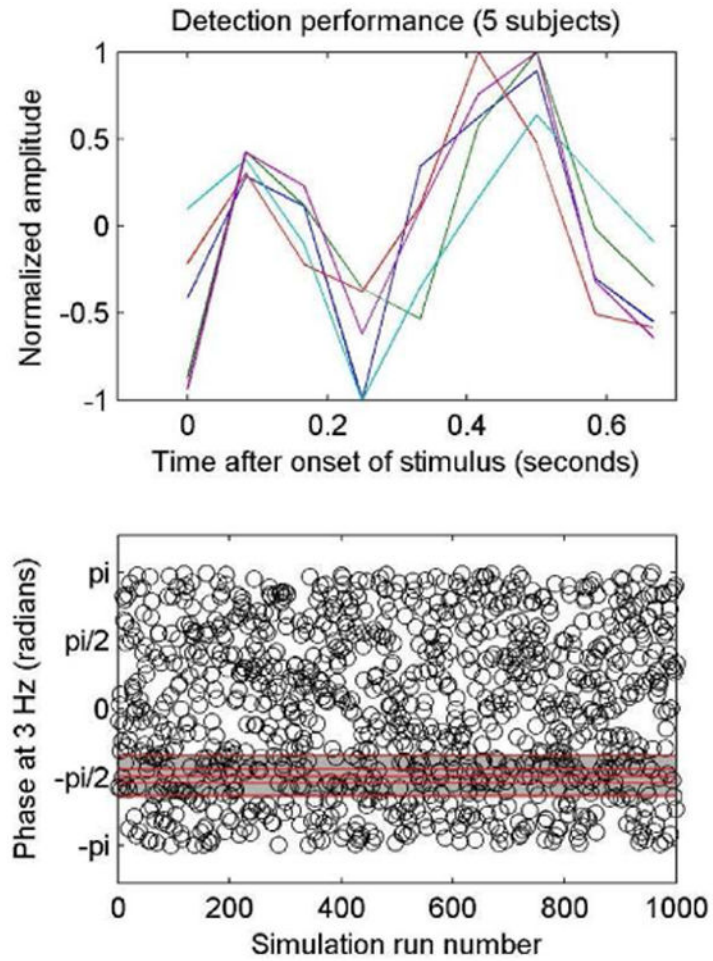


Figure 4.

Top panel shows signal-detection curves for 5 subjects normalized to a peak of unity (data taken from Fig. 3). The red lines in the bottom panel show phase spectra calculated from the Fourier transform of the curves in the top panel. Note that all are within a half a radian (gray rectangle) of $-\pi/2$, which is antiphase to the expected modulation waveform (red curve in the lower right panel of Fig. 3).

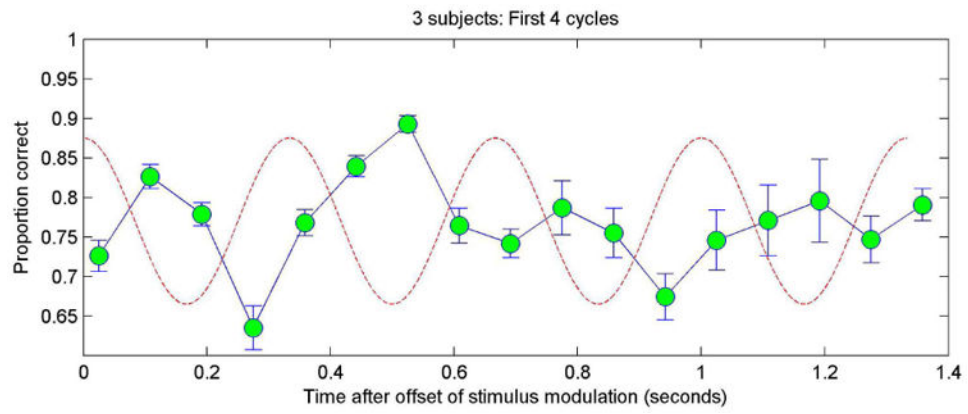


Figure 5. Tone detectability as a function of time after offset of noise modulation, showing four modulation cycles. Average performance across three participants is shown. NOTE: the first two cycles from the first experiment (data presented above), the second two cycles from the second experiment involving the same 3 participants. Error bars represent 1 standard error.

Table 1

Pairwise t-test comparisons between all temporal positions

	t1	t2	t3	t4	t5	t6	t7	t8	t9
t1		**				*	**		
t2	**		*	*			**	*	**
t3		*					**		*
t4		*	*		*	**	**		
t5						*	**		
t6									*
t7								**	**
t8							**		*
t9		**	*			*	***	*	

* <0.05;

** <0.01;

*** <0.001