Neural decoding of bistable sounds reveals an effect of intention on perceptual

organization

Alexander J. Billig[1], Matthew H. Davis[1], and Robert P. Carlyon[1]

[1]MRC Cognition and Brain Sciences Unit, University of Cambridge, Cambridge, UK, CB2

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Corresponding Author: Alexander J. Billig, Brain and Mind Institute, The University of

Western Ontario, London, ON, Canada, N6A 3K7. Email: ajbillig@gmail.com

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30   **Abstract**

Auditory signals arrive at the ear as a mixture that the brain must decompose into

distinct sources, based to a large extent on acoustic properties of the sounds. An

important question concerns whether listeners have voluntary control over how many

sources they perceive. This has been studied using pure tones H and L presented in

the repeating pattern HLH-HLH-, which can form a bistable percept, heard either as

an integrated whole (HLH-) or as segregated into high (H-H-) and low (-L--)

sequences. Although instructing listeners to try to integrate or segregate sounds

affects reports of what they hear, this could reflect a response bias rather than an

underlying perceptual effect. We had human listeners continuously report their

perception of such sequences while we recorded neural activity using magneto-

encephelography. During neutral listening, a classifier trained on patterns of neural

activity distinguished between periods of integrated and segregated perception. In

other conditions, participants tried to influence their perception by allocating attention

either to the whole sequence, or to a subset of the sounds. They reported hearing the

desired percept for a greater proportion of time than when listening neutrally.

Critically, neural activity supported these reports; stimulus-locked brain responses in

auditory cortex were more likely to resemble the signature of segregation when

participants tried to hear segregation than when attempting to perceive integration.

These results indicate that listeners can influence how many sound sources they

perceive, as reflected in neural responses that track both the input and its perceptual

organization.

Significance Statement

Can we consciously influence our perception of the external world? We address this

question using sound sequences that can be heard either as coming from a single

source, or as two distinct auditory streams. Listeners reported involuntary changes in

their perception between the two interpretations while we recorded neural activity to

identify signatures of integration and segregation. They also indicated that they could,

to some extent, choose between these alternatives. This claim was supported by

corresponding changes in responses in auditory cortex. By linking neural and

behavioral correlates of perception we demonstrate that the number of objects we

perceive can depend not only on the physical attributes of our environment, but also

on how we intend to experience it.

Introduction

For us to make sense of our environment, the brain must determine which elements of

energy arriving at the sensory organs arise from the same source and should therefore

be perceptually grouped. In audition, the less rapidly that sequential sounds change in

one or more physical quantities, such as frequency, intensity, or spatial location, the

more likely they are to be integrated and represented as a single perceptual object or

stream (Moore & Gockel, 2012; van Noorden, 1975). The processes that underlie

integration and segregation are affected not only by these stimulus features but also

by internal states of the listener, such as the degree to which they are attending to the

sounds (Carlyon et al., 2001; Sussman et al., 2002; Snyder et al., 2006; Billig and

Carlyon, 2015), and by whether the stimuli correspond to a familiar speaker

(Johnsrude et al., 2013) or word (Billig et al., 2013). The extent to which observers

can voluntarily influence how they perceptually organize the outside world is unclear

and bears on questions of whether and how higher-level cognition can influence

perception (Fodor, 1983; Pylyshyn, 1999; Firestone and Scholl, 2015).

A common stimulus for investigating auditory perceptual organization is a repeating

pattern of pure tones of high (H) and low (L) frequencies, such as that shown in

Figure 1A. For lower frequency separations and presentation rates the sounds tend to

be heard as integrated in a single stream that forms a distinctive galloping rhythm. At

greater frequency separations and presentation rates the H and L tones typically form

two segregated streams (van Noorden, 1975). For a range of stimulus parameters,

perception can alternate between the two percepts every few seconds, usually after a

longer initial integrated phase (Carlyon et al., 2001; Denham et al., 2013; Pressnitzer

& Hupé, 2006; Figure 1B).

94   [FIGURE 1 ABOUT HERE]

For such ambiguous sequences, listeners report being able to exert a degree of control

over hearing integration or segregation (van Noorden, 1975; Pressnitzer and Hupé,

2006; Micheyl and Oxenham, 2010; Farkas et al., 2016). However, subjective

responses may be affected by post-perceptual processes and biases, such as shifts in

decision criteria (Green and Swets, 1966) or attempts to meet the perceived aims of

the experiment (Orne, 1962). To the extent that they vary with a listener's percept,

indirect behavioral or neural measures can bypass such issues. For example, several

electro- and magneto-encephalography (EEG/MEG) studies have detected more

positive auditory cortical responses approximately 60-100 ms following the onset of

the middle tone in such triplets during reports of segregation compared to integration

(Gutschalk et al., 2005; Snyder et al., 2006; Hill et al., 2012; Szalárdy et al., 2013a).

We argue that these objective neural measures can also shed light on the neural stages

of processing that underlie any genuine effect of intention on perception.

Here we combine subjective and objective measures to demonstrate an effect of

intention on perception, reflected in evoked responses in auditory cortex. To do so we

measure neural activity with EEG/MEG as participants listen neutrally to HLH-

sequences (Figure 1A) and report spontaneous changes in their perception (Figure

1B). We derive a univariate marker of perceptual organization in the auditory evoked

field at the group level, but also make use of multiple temporal features in the neural

response to train multivariate percept classifiers for each participant. We then study

the relative occurrence of these neural signatures when participants actively try to

promote integration (by attending to the whole pattern) or segregation (by attending

exclusively to tones of one frequency). This allows us to establish whether their

reports of successfully influencing their percept are supported by and reflected in

stimulus-locked activity in auditory cortex, or are instead more likely to have a post-

perceptual locus.

Materials and Methods

Participants

Data were collected in two separate experimental settings. Twenty-five participants

took part in a sound booth (Setting 1), for the purposes of (a) ensuring that stimulus

parameters gave rise to integrated and segregated percepts in approximately equal

measure, and (b) screening participants before EEG/MEG recording to ensure that

they could experience both percepts. Twenty-two of these participants also took part

in the EEG/MEG lab (Setting 2), between 1 and 34 days later. Two further

participants took part in Setting 2 only, after screening with an online test. All 27

participants across both settings were aged 18-40 (mean age = 28.56, 12 females),

right-handed and reported no neurological or developmental disorders. They were

recruited from the MRC Cognition and Brain Sciences Unit participant panel or by

word of mouth, and were paid for their time. One participant, whose results were not

qualitatively different from the remainder of the group, had a threshold of 30 dB HL

at 1500 Hz in the left ear. All other participants had normal hearing (<25 dB HL pure

tone thresholds over the range of the stimuli, 1000-2000 Hz). All experimental

procedures were approved by the Cambridge Psychology Research Ethics Committee.

Stimuli

Sequences of 250 HLH triplets were presented diotically, where H (high) and L (low)

were 100-ms pure tones (Figure 1A). The frequency of the H tone was fixed at 1000

Hz (Setting 1) or 1017 Hz (Setting 2), except for the final H tone in the final triplet

when it was 250 Hz. The choice of 1017 Hz in Setting 2 was to avoid possible

contamination by harmonics of the 50 Hz line noise. The 250 Hz tone was low

enough in frequency to be detectable on a low-pass filtered auxiliary channel of the

MEG recording set-up in Setting 2, and was included to enable neural recordings to

be time-locked to the stimulus. The L tone in a given sequence was lower than that of

the H tone by an amount (Δf) of either four or six semitones (both settings). Silent

intervals of 50 ms separated tones within a triplet, and silent intervals of 200 ms

separated one triplet from the next, giving sequences of 150 s duration. These stimuli

were chosen to match Experiment 2 of Gutschalk et al. (2005).

Filler stimuli lasting a total of 40 s were created to separate experimental sequences.

These consisted of 5,005 ms silence, followed by a 100-ms 250-Hz tone (a time-

locking signal, with the same purpose as that described in the previous paragraph).

This was followed by 1,900 ms of silence, then by 33 pure tones, each of 100 ms

duration with 50 ms of silence between tones. The frequencies of these tones were

selected at random from a log-rectangular distribution from 200-2000 Hz. Their

purpose was to interfere with memory of the previous sequence in an effort to

minimize context effects, such as those described by Snyder et al. (2009). The filler

stimulus continued with 22,945 ms of silence, another 100-ms 250-Hz tone (to warn

the participant that the next experimental sequence was about to begin) and a final

5,000 ms of silence. All tones in the experimental sequences and filler stimuli

included 10-ms linear onset and offset ramps, and were generated digitally at a

sample rate of 44100 Hz with 16-bit resolution.

Experimental procedures

In Setting 1, participants were seated in a double-walled sound-insulated room and

sounds were presented over Sennheiser HD650 headphones at a level of 55 dB SPL.

In Setting 2, participants sat under the dewar of a VectorView system (Elekta

Neuromag) while MEG and EEG activity was recorded (see "EEG and MEG

acquisition and pre-processing" section for details of preparation and recording). In

this setting, sounds were presented through tube headphones with silicone inserts at

50 dB above the participant's 1000 Hz pure tone hearing threshold. Using their right

hand, participants pressed one computer key (Setting 1) or button box button (Setting

2) when hearing an integrated, galloping triplet pattern, and another when hearing the

tones segregate into two isochronous sequences (Figure 1B). The screen indicated

their most recent response, which corresponded to their current percept. They were

told to make a selection as soon as possible after the sequence began, and to make

further responses whenever their percept changed. There were four conditions with

different instructions. In "Neutral" sequences participants were instructed to let their

perception take a natural course. In "Attempt Integration" sequences they tried to

promote the Integrated percept by attending to the whole pattern. In "Attempt

Segregation" sequences they tried to promote the Segregated percept by attending

either to the H tones ("Attend High") or the L tones ("Attend Low").

The experiment consisted of two (Setting 1) or four (Setting 2) blocks. Each block

contained five sequences: two Neutral, one Attempt Integration, one Attend High and

one Attend Low. In Setting 1 the order of instruction conditions was the same in both

blocks for a given participant; in Setting 2 this order was reversed for the final two

blocks. The two neutral sequences in a block never occurred consecutively, and Δf

alternated between four and six semitones from sequence to sequence. An on-screen

message specified the instruction prior to and throughout each trial. Response

key/button mapping, and order of instruction and Δf conditions were balanced across

participants. Participants relaxed between sequences and took breaks of at least a

minute between blocks (while remaining under the dewar in Setting 2). During

experimental trials in Setting 2 they were instructed to keep their eyes open and to

maintain fixation on a cross in the centre of the screen, or elsewhere if more

comfortable, to minimize alpha power and artefacts from eye movements. In Setting

2, participants' head positions were checked at the start of each block, and their

position adjusted (to minimize loss of MEG signal) if they had dropped by a

centimetre or more. Testing lasted approximately 30 min in Setting 1 and 60 min in

Setting 2.

Before the experiment, the concept of streaming was explained using HLH- patterns

with Δf of 0, 5 and 12 semitones. Participants practiced reporting their percept while

listening neutrally. They were then told that they may be able to influence their

percept by attending either to the whole pattern or to one or other sets of tones; these

conditions were also practiced. Participants were told that it was far more important to

be honest and accurate in their responses than to be successful in their attempts to

influence their percept. In Setting 2, practice and experimental blocks occurred after

electrode preparation and head position digitization (described in the "Experimental

design and statistical analysis - EEG and MEG acquisition and pre-processing"

section). The two participants who had not taken part in Setting 1 completed an online

training session to familiarize themselves with the stimuli and percept reporting

process, and to practice trying to influence their percept. Instructions were repeated in

person immediately prior to the experiment. Those participants who had taken part in

Setting 1 more than a week previously also completed the online training as a

refresher.

EEG and MEG acquisition and pre-processing

Magnetic fields were recorded using a VectorView system (Elekta Neuromag) with

one magnetometer and two orthogonal planar gradiometers at each of 102 locations.

Electric potentials were recorded concurrently using seventy Ag-AgCl sensors

arranged in the extended 10-10% configuration, fitted to the scalp using an electrode

cap (Easycap) and referenced to an electrode on the nose, with a ground electrode on

the right cheek. Head position was continuously monitored using five head position

indicator (HPI) coils. Electro-cardiographic (ECG) and horizontal and vertical

electro-oculographic (EOG) activity was recorded with three pairs of electrodes. The

positions of the EEG sensors, HPI coils and approximately 100 additional head points

were digitized with a 3D digitizer (Fastrak Polhemus), relative to three anatomical

fiducial points (the nasion and both pre-auricular points). Data were acquired with a

sampling rate of 1000 Hz and a high-pass filter of 0.01 Hz. For the magnetometer and

gradiometer recordings, the temporal extension of Signal Space Separation in

MaxFilter was used to identify bad channels, suppress noise sources, and compensate

for head movement. For all sensor types, additional noisy channels were identified for

each participant based on observations during recording and offline visual inspection.

Line noise at 50 Hz and its harmonics was removed using adaptive multitaper

regression implemented in the EEGLAB plugin CleanLine, and all activity

downsampled to 250 Hz.

To separate brain signals of interest from physiological and other noise sources, an

independent components analysis (ICA) was performed in EEGLAB. In preparation,

timecourses of all channels were visually inspected, and sections containing artefacts

were removed. These included SQUID jumps, channel pops, and muscle activity, but

excluded eye blinks/movements and cardiac artefacts, which are addressed in the

ICA. EEG channels were considerably noisier than magnetometers and gradiometers,

and did not improve the quality of the ICA. They were therefore discarded, and

subsequent analyses were restricted to magnetometers and gradiometers only. These

channels were initially high-pass filtered at 0.5 Hz (6 dB cut-off, 1 Hz transition band,

FIR windowed sinc filter) to impose the stationarity assumed by ICA. Infomax ICA

was run in EEGLAB, with sphering across magnetometers and gradiometers and

including sub-Gaussian components. The weights from the ICA were then applied to

another copy of the data that had been low-pass filtered at 30 Hz (6dB cut-off, 6.667

Hz transition band, FIR windowed sinc filter) and high-pass filtered at 0.278 Hz (6 dB

cut-off, 0.556 Hz transition band, FIR windowed sinc filter). This high-pass filter was

selected for reasons explained in the next paragraph.

The filtered data, with ICA weights applied, were divided into 600-ms epochs, each

beginning at the start of an HLH- triplet. Epochs beginning less than 1500 ms after a

button press (or the start of the sequence) or ending less than 1500 ms before a button

press (or the end of the sequence) were excluded from analyses. This minimized

neural and muscular activity related to movement and removed periods around

transitions when the reported percept was less likely to be reliable. Baseline

correction was not performed due to the repeating nature of the stimulus precluding a

sufficient silent period between triplets, which meant that neural responses from one

epoch were likely to carry over to the next. Due to the exclusion of epochs close to

reported perceptual switches, any such influence should arise solely from triplets with

the same (reported) perceptual state, and epoch time can therefore be thought of as

circular (see Hill et al. (2012) for a similar approach). The high-pass filter of 0.278 Hz

corresponds to a 3600-ms time period, the shortest possible interval between retained

epochs corresponding to different perceptual reports. The relatively conservative

approach of epoch rejection, necessary for tapping periods that were as perceptually

stable as possible, led to a median retention rate of 58% (2900 epochs) per participant,

comparable to that in Hill et al. (2012).

Further analyses applied to data from individual participants selected the single

independent component that (a) had a neural (as opposed to artefactual) source, as

revealed by inspection of scalp topographies and (b) showed the maximum mean

back-projected power in the evoked response, over all retained epochs. As the output

of ICA is arbitrary with respect to the polarity of the scalp topography, waveforms

were inspected for each participant and inverted as necessary such that the first

pronounced turning point in the waveform (peaking between 50-90 ms and possibly

corresponding to the canonical P1 response to the first H tone of a triplet) was a local

maximum.

Source reconstruction

To determine the underlying brain sources corresponding to each selected

independent component, single equivalent current dipole models were fitted to the

gradiometer data at a participant level using the VB-ECD approach in SPM12, with

no prior location or orientation constraints. These reconstructions made use of single

shell forward models based on participant-specific T1-weighted structural MRI scans.

Sensor positions were projected onto each participant's MRI by minimizing the sum

of squared differences between the digitized fiducials and MRI scan fiducials, and

between the digitized head shape and the individual scalp mesh. The VB_ECD

routine uses a variational Bayes approach to iteratively optimize location and

orientation parameters of a fitted dipole. The reconstruction that accounted for the

maximum variance in scalp data out of 50 iterations was selected for each participant.

Experimental design and statistical analysis

Sample size justification

No published research has used the same approach to test for intention effects with

the same stimuli, however effect sizes for two relevant findings can be estimated from

previous studies: (a) an intention effect on behavioral streaming measures of $\eta^2=.70$

(Pressnitzer & Hupé, 2006) and (b) a percept effect on MEG evoked responses of

$\eta^2=.43$ (Gutschalk et al., 2005). Of the two effects, the latter would require the largest

sample size to detect, namely 18 participants for 90% power. We tested 24

participants in the MEG setting; this allowed for drop-outs and accounted for possible

over-estimation of effect sizes due to unreported null findings.

Behavioral analyses

As there were no significant differences in the mean percentage of segregation

reported across the sound booth and EEG/MEG lab settings (t(15)=1.38, p=.189,

d=0.23, 95% CI [-0.20 0.04], tested on the 16 participants with no conditions in either

setting in which the percentage of segregation was 0 or 100), behavioral data were

combined across the two settings. Of the 27 participants, two (both tested only in

Setting 1) were excluded from behavioral data analyses. Both had at least one Δf x

instruction condition with no sequences that met the following criteria: (i) the first

reported phase was integrated (ii) at least two completed subsequent phases were

reported. These criteria were necessary to allow separate analysis and comparison of

the duration of initial-integrated, subsequent-integrated and segregated phases.

Percentages of segregation for all remaining participants were logit-transformed and

phase durations were log-transformed before being submitted to repeated-measures

ANOVAs for analysis as a function of Δf and instruction. These transformations

typically produced data with normally distributed residuals. When this was not the

case, non-parametric tests were also conducted; these gave rise to the same qualitative

pattern of results and are not reported separately. Mean percentages/durations were

calculated on the transformed scale, then converted back to percentages/seconds for

reporting. Null hypothesis significance testing was applied, with an alpha value of

.05. Degrees of freedom were adjusted for asphericity as appropriate using the

Huynh-Feldt correction (uncorrected degrees of freedom are reported for clarity).

Univariate neural analyses

Epochs in the neutral condition were averaged for each combination of Δf and

reported percept, for each participant. To maximize power, epochs occurring prior to

the first percept report were labelled as Integrated, and the first Integrated phase of a

sequence was not considered separately from the remaining integrated phases. The

exclusion of any epochs before the first segregated report (in line with some

researchers' suggestions to treat these separately (Denham et al., 2013)) led to

qualitatively similar results. One participant, who had only five valid epochs in one Δf

x percept cell in the neutral condition, was excluded from subsequent analyses of

neural data. All other participants had at least 55 valid epochs per Δf x percept cell in

the neutral condition (the mean across participants of number of epochs in smallest

cell was 145). To assess neural activity as a function of percept without stimulus

confounds, the timecourses of the two Δf conditions were averaged within each

percept before statistical analysis. Percept differences were similarly partialled out of

analyses of neural activity as a function of Δf.

Statistical differences between percepts and frequency separations in the neutral

condition were assessed using a cluster-based permutation method (Maris and

Oostenveld, 2007). Within-subjects *t*-tests were conducted at each timepoint, and the

largest contiguous cluster of values all exceeding a critical *t*-value (corresponding to

an alpha value of .05) was selected for further analysis. Cluster significance was

assessed by comparison to a null distribution generated by randomly permuting the

labels of condition averages 1000 times within each subject, and using an alpha value

of .05.

Epochs in the Attempt Integration, Attempt Segregation (Attend High), and Attempt

Segregation (Attend Low) were averaged within each Δf, without regard to reported

percept. Differences over the temporal cluster of interest from the neutral condition

were derived for each of the following contrasts: (a) ½ * Attempt Segregation (Attend

High) + ½ * Attempt Segregation (Attend Low) – Attempt Integration, (b) Attempt

Segregation (Attend High) – Attempt Integration, (c) Attempt Segregation (Attend

Low) – Attempt Integration, (d) Attempt Segregation (Attend High) – Attempt

Segregation (Attend Low). In all cases, the two Δf conditions were given equal

weight. Paired t-tests were conducted on these differences.

To test whether effects of intention on univariate neural responses in the non-neutral

conditions were as large as would be expected based on perceptual reports, and under

the assumption that the neural signature of percept in the neutral condition also

applied in the non-neutral conditions, the following calculations were made. The

percentages of each percept reported in each non-neutral condition for each Δf and

participant were applied to the relevant mean neural response from the neutral

condition. Simulated and observed values were compared using a paired t-test, with

an alpha value of .05.

Multivariate neural analyses

Epochs were labelled and participants excluded as outlined in the "Experimental

design and statistical analysis - Univariate neural analyses" section. Support Vector

Machines (SVMs) with linear kernels were trained to classify Integrated versus

Segregated trials in the neutral condition for each Δf and participant, using an adapted

version of the DDTBOX package (Bode et al., 2017) in MATLAB. To ensure

unbiased classifiers, random sub-sampling within each SVM was used to match the

number of epochs across classes. Five-fold cross-validation was applied, and the

subsampling and cross-validation process was repeated 100 times. Features were the

non-standardized values of the neural response at the 150 sampled time points of each

600-ms epoch (arising from the 250 Hz sampling frequency), and the cost parameter

(C) was set as 1. Classifier performance in the neutral condition was assessed for each

participant by comparing classified versus actual labels and averaging the percent

correct over the 5x100 = 500 iterations, and over Δf conditions. Group classification

accuracy was tested against the 50% chance level using a t-test with an alpha value of

.05. Feature weights were obtained from the SVM training functions, and corrected

using the method of Haufe et al. (2014), which removes strongly weighted but

theoretically irrelevant noise features. These were normalized across subjects then

averaged over Δf for plotting. The 500 trained SVMs for each Δf and participant were

also used to classify all epochs in the non-neutral conditions, regardless of percept

report. The percentage classified as segregated was compared across non-neutral

conditions using within-subjects t-tests with an alpha value of .05, for the same

contrasts as outlined in the "Univariate neural analyses" section.

To test whether task-related differences in the percentage of epochs classified as

segregated was as high as would be expected based on subjective reports, it was

necessary to take into account the accuracy of the trained classifiers in the neutral

condition. The percentage of reports of segregation for each participant, frequency

separation, and task was multiplied by (neutral classification accuracy – 50)/50 (i.e.

the neutral classification accuracy above chance, as a proportion from -1 to 1). The

expected task-related difference in the percentage of epochs classified as segregated

was derived for each participant and frequency separation, by taking the average of

these adjusted percentages of segregated reports over the two Attempt Segregation

conditions and subtracting the adjusted percentage of segregated reports in the

Attempt Integration condition. These expected difference values were then averaged

over frequency separations, and compared to the observed differences using a paired

t-test, with an alpha value of .05.

Results

Behavioral results

As shown in Figure 2A, segregation was reported for a greater proportion of time for

the larger than for the smaller Δf for all tasks. This arose from a combination of

shorter initial integrated phases (Figure 2B), shorter subsequent integrated phases

(Figure 2C), and longer segregated phases (Figure 2D). All of these effects were

statistically significant (Figure 2A: $F(1,24) = 34.89$, $p=4\times10^{-6}$, $\eta^2_p=.59$, 95% CI [.48

.72]. Figure 2B: $F(1,24)=46.58$, $p<.001$, $\eta^2_p=.66$, 95% CI [.58 .77]. Figure 2C:

$F(1,24)=15.28$, $p<.001$, $\eta^2_p=.39$, 95% CI [.18 .58]. Figure 2D: ($F(1,24)=11.28$,

$p<.001$, $\eta^2_p=.32$, 95% CI [.09 .58]).

[FIGURE 2 ABOUT HERE]

Importantly, the percentage of time each percept was reported was also affected by

the task instructions ($F(1,24)=51.55$, $p<.001$, $\eta^2_p=.68$, 95% CI [.58 .80]; Figure 2A).

This effect was reflected in extended phases of the intended percept (although not to a

significant extent for non-initial integrated phases) and shortened phases of the

unintended percept, in comparison to the Neutral condition (Figure 2B, 2C, 2D; see

Table 1 for statistics). Focusing on tones of a single frequency to promote segregation

had a larger effect on the percentage of time hearing segregation than trying to hold

the three tones in a triplet together (the black lines are closer to the blue lines than to

the green lines in Figure 2A; $t(24)=3.03$, $p=.006$, $d=0.67$, 95% CI [0.17 1.17]).

However, there was no effect of attending to the high versus the low tones during

segregated listening ($t(24)=1.29$, $p=.208$, $d=0.27$, 95% CI [-0.15 0.69]).

Table 1. Statistics for effects of intention on phase durations (compared to the Neutral condition)

Task	Phases	t-value	p-value	d	d 95% CI
Attempt Integration	Initial integrated	3.75	.001	0.40	[0.15 0.65]
	Subsequent integrated	1.75	.094	0.17	[-0.03 0.37]
	Segregated	3.90	<.001	0.56	[0.22 0.90]
Attempt Segregation (Attend High)	Initial integrated	5.30	<.001	0.70	[0.36 1.05]
	Subsequent integrated	4.95	<.001	0.85	[0.42 1.28]
	Segregated	2.62	.015	0.35	[0.05 0.64]
Attempt Segregation (Attend Low)	Initial integrated	3.70	.001	0.63	[0.23 1.03]
	Subsequent integrated	4.13	<.001	0.66	[0.27 1.04]
	Segregated	3.67	.001	0.66	[0.24 1.08]

Univariate neural results

We then decomposed recordings of each participant's neural activity to find the

independent component with the largest evoked response after averaging over 600-ms

(triplet-length) windows. The timecourse of this component was extracted for each

percept, independent of Δf (Figure 3A). Source localization established left

hemisphere generators for these components in seven participants, and right

hemisphere generators in the remaining sixteen. After projecting all sources to a

single hemisphere, the mean reconstructed source was located in auditory cortex near

posteromedial Heschl's gyrus (MNI coordinates [+/-51, -23, +4]; Figure 3B). A

univariate analysis on the time courses of these components revealed a time window

at 212-256 ms post triplet onset (62-106 ms post L tone onset) when epochs in the

neutral condition reported as segregated evoked a significantly more positive response

than those reported as integrated, independent of Δf (cluster-based permutation test,

$p=.021$; window-specific test, $t(22)=4.18$, $p<.001$, $d=0.38$, 95% CI [0.16 0.60]; Figure

3C).

475   [FIGURE 3 ABOUT HERE]

The effect of intention on the neural response in this window was determined by

subtracting the mean over all epochs during attempts at integration from the mean

over all epochs during attempts at segregation, regardless of reported percept. The

group difference was significantly greater than zero ($t(22)$=2.24, p=.035, d=0.19, 95%

CI [0.01 0.37]; Figure 3D, middle), paralleling the percept comparison in the neutral

condition (Figure 3D, left) and supporting participants' reports that they heard more

segregation when they tried to do so than when they tried to hear integration. This

effect is unlikely to be driven by attention-related modulations of neural responses to

particular tones independent of perceptual organization; the conditions in which

attention was focused on the H or the L tones did not differ significantly from each

other ($t(22)$=0.29, p=.772, d=0.03, 95% CI [-0.18 0.24]; Figure 3D, right).

Importantly, there was also no evidence for a residual response bias; the magnitude of

the neural difference in the non-neutral conditions was similar to that expected if all

reports in those conditions were accurate ($t(22)$=0.10, p=.919, d=0.02, 95% CI [-0.44

0.49]).

Multivariate neural results

The difference waveform in the neutral condition (Figure 3C) indicated that multiple

time windows might be informative in distinguishing between integrated and

segregated percepts, beyond the 212-256 ms window selected in the univariate

analysis above. To make use of information across the entire epoch, we sought

multivariate temporal patterns that distinguished between integrated and segregated

percepts at a single-trial level, and which were allowed to vary across participants.

Linear Support Vector Machines (SVMs) trained for each Δf and participant (Figure

4A) achieved classification accuracy significantly above chance ($t(22)=5.33$, $p<.001$,

$d=1.55$, 95% CI [0.86 2.72]; Figure 4B). Classification was driven by responses in

multiple time windows, including that identified in the univariate analysis (Figure

4C).

507   [FIGURE 4 ABOUT HERE]

The SVMs trained on neutral epochs were then used to classify epochs in the other

conditions. Paralleling the univariate results, a greater percentage of epochs were

classified as segregated when participants attempted segregation than when they tried

to integrate the sounds ($t(22)=3.79$, $p=.001$, $d=1.10$, 95% CI [0.55 1.90]; Figure 4D,

left). Again, this was not driven by epochs in which tones of one particular frequency

were attended; the percentage of epochs classified as segregated was similar whether

participants attended to high or low tones ($t(22)=0.41$, $p=.688$, $d=0.11$, 95% CI [-0.46

0.75]; Figure 4D, right).

The task-related difference in the percentage of epochs classified as segregated (mean

1.9%) was more than an order of magnitude smaller than the difference in reported

proportions (mean 36.6%). This discrepancy was due to non-perfect classifier

performance; although accuracy was above chance (50%), the mean was only 52.6%

and the maximum across participants 56.3%. After taking into account the accuracy

of each classifier, the task-related difference in the percentage of epochs classified as

segregated was no different from that expected if all percept reports in the non-neutral

conditions were accurate ($t(22)=0.13$, $p=.896$, $d=0.03$, 95% CI [-0.47 0.53]). In line

with the univariate analysis, there was therefore no evidence for a residual response

bias.

The effect of intention determined by the multivariate analysis was larger and more

reliable than that from the univariate analysis. The more flexible approach was able to

exploit the data of participants whose neural activity did not align with the group

percept signature in the 212-256 ms time window. For example, one participant's

percept in the neutral condition could be decoded above chance, based primarily on

activity occurring around 424 ms post stimulus onset (Figure 4B, orange trace; Figure

4C, orange circle).

Discussion

Our findings demonstrate that listeners can exert intentional control over how many

objects they perceive in an ambiguous auditory scene. Differences in auditory cortical

responses during attempts to hear repeating patterns of pure tones as an integrated

whole versus segregated streams were consistent with signatures of these percepts

obtained during a neutral listening condition. These differences supported listeners'

subjective reports that they can, to some extent, "hear what they want to hear".

Indexing low-level perception

We argue that the activity measured during neutral listening relates to the percept

rather than to decisions made during the process of reporting it. Variability across

participants and the inherent uncertainty of localization based on MEG preclude

ascribing a primary versus non-primary auditory cortical locus; our source

reconstruction appears consistent with either of these. However, it seems unlikely that

post-perceptual decision-related activity would originate from auditory regions and be

so consistently timed from the onset of each stimulus. Furthermore, we excluded

epochs surrounding button presses to minimize the contribution of activity relating to

motor planning or execution. We therefore take the neutral neural signature to reflect

perceptual experience.

The use of bistable stimuli to probe perception avoids acoustic confounds. Although

we presented stimuli with two different frequency separations, the key comparisons of

neural activity were between alternative percepts of identical sounds. This contrasts

with Gutschalk et al. (2005), for example, in which data were collapsed across HLH-

patterns with two different intermediate frequency separations before being analyzed

for neural correlates of perception.

Our interpretation of activity in the non-neutral conditions assumes that the neural

response carried more information about perception than about the instructions

themselves, which differed in terms of how listeners were to attend to the sounds.

Selective attention is known to affect the evoked response to tones even when

perceptual organization is fixed (Hillyard et al., 1973; Näätänen et al., 1978). Such

modulations would presumably be maximally different across the two sub-conditions

in which participants attended exclusively to either the H or L tones, rather than

between one of these sub-conditions and the case when listeners attended to all of the

tones. However, we found no difference between attending to H and L tones over the

time window of interest in the univariate analysis, nor in the percentage of epochs

classified as segregated in the multivariate analysis. We therefore argue that attention

alone (without concomitant changes in perceptual organization) cannot account for

the observed neural effects.

Another important feature of our design was the simultaneous collection of percept

reports and neural data, allowing us to draw direct associations between the two.

Some previous studies have inferred integration or segregation using measures that

are sensitive to stimulus manipulations that also affect perceptual organization, such

as the mismatch negativity (Sussman et al., 1999; Winkler et al., 2006; Carlyon et al.,

2010) or performance on a deviant detection task (Carlyon et al., 2010; Micheyl and

Oxenham, 2010; Billig et al., 2013; Spielmann et al., 2014). However such measures

are influenced by additional factors (Divenyi and Danner, 1977; Spielmann et al.,

2013, 2014; Sussman et al., 2013; Szalárdy et al., 2013b), and the degree to which

they alone can provide a reliable indication of perceptual organization over the course

of sustained bistable stimulation is not clear.

Implications for auditory scene analysis

The more positive response for segregation compared to integration 62-106 ms after

the onset of the L tone was consistent with previous findings (Gutschalk et al., 2005;

Hill et al., 2012; Szalárdy et al., 2013a). It may reflect an increased P1m response to

the L tone during segregation, due to a release from adaptation by responses to the

previous H tone as neuronal receptive fields narrow and segregation occurs (Fishman

et al., 2001; Gutschalk and Dykstra, 2014). However, our results do not depend on

this interpretation; given the continuous stimulation paradigm it may be unclear which

tone generates this neural response. Furthermore, our participant-specific

classification analysis indicated that this time window may not be the most diagnostic

of percept for all individuals. Variability across listeners may arise from distinct

listening strategies, or reflect differences in how multiple components from repeated

sounds summate to an aggregate measured signal. In recent years, multivariate

techniques such as representational similarity analysis have provided insight into the

fine spatial patterns representing stimulus information in the brain (Haxby et al.,

2001; Kriegeskorte et al., 2008). Here we applied a different form of multivariate

analysis – classification in the temporal domain - to reveal individualized percept-

specific patterns in neural activity (see also Wilbertz et al., 2014, Reichert et al., 2014,

for classification of bistable visual perception). Although we focused on stimulus-

locked responses in auditory cortex, correlates of stream segregation and of

spontaneous switches in bistable sequences have been observed in other brain regions,

including inferior colliculus, thalamus, intraparietal sulcus, insula, and cerebellum

(Cusack, 2005; Schadwinkel and Gutschalk, 2010; Hill et al., 2011; Kashino and

Kondo, 2012). Whether any of these play a role in voluntary perceptual switches will

be a question for future study.

A distinction has been drawn between primitive and schema-based processes of

perceptual organization (Bregman, 1990). Primitive processes automatically partition

a scene based on its physical properties, whereas schema-based processes select

elements based on attention or prior knowledge. One might expect different neural

instantiations of the outcomes of these processes; however, we found the same

segregation signature regardless of whether listeners allowed their perception to take a

natural course, deliberately attended to the H tones, or deliberately attended to the L

tones. We argue that the neural realization of an auditory scene consists not only of

distinct representations of attended and unattended streams to different degrees of

fidelity (Mesgarani and Chang, 2012; Puvvada and Simon, 2017) but also of markers

of whether any segregation has occurred at all (c.f. Gandras et al. 2017; Szalárdy,

Winkler, et al. 2013).

We asked participants to try to influence their percept by attending either to a subset

of the tones, or to all of them. The former approach may succeed by narrowing

receptive fields of auditory cortical neurons such that different populations respond to

the tones of each frequency (Fritz et al., 2007; Ahveninen et al., 2011), or by

introducing a perceived loudness difference between H and L tones (van Noorden,

1975; Dai et al., 1991). In contrast, repeatedly shifting attention across frequencies

may promote integration by disrupting these effects. The size of the change in reports

from the Neutral to the Attempt Segregation condition was greater than that from the

Neutral to the Attempt Integration condition. This was not the case in previous studies

(Pressnitzer and Hupé, 2006; Micheyl and Oxenham, 2010), a fact that may reflect

differences in stimuli, or in how instructions were interpreted. We also note that in

our experiment, volitional control similarly affected reported durations of intended

and unintended phases, whereas Pressnitzer and Hupé (2006) found that phases of

unwanted percepts were curtailed to a greater degree than target phases were

extended. Listeners in that study may have used additional strategies to shorten

segregated phases, such as diverting cognitive resources away from the tone sequence

(Carlyon et al., 2003). Phase duration distributions have informed modelling of

auditory scene analysis (Mill et al., 2013; Rankin et al., 2015) and prompted parallels

to be drawn between different forms of bistability across sensory modalities

(Pressnitzer and Hupé, 2006). We emphasize that the interaction between stimulus

characteristics and high-level factors such as attention, which may differ across

bistable phenomena, must be considered in general accounts of how the brain handles

perceptual ambiguity (van Ee et al., 2005; Kogo et al., 2015).

Implications for cognitive influences on perception

There has been much debate about whether attention-mediated effects of knowledge

and goals on perceptual experience should count as true cases of cognitive penetration

of perception (Firestone and Scholl, 2015; Gross, 2017; Lupyan, 2017). Some

researchers argue that attention simply acts on the input to perception rather than on

662 its mechanisms. For example, focusing on a particular spatial location (Bonnel et al.,

663 1987), colour (Green and Anderson, 1956), or frequency (Dai et al., 1991) allows for

664 the selection of a subset of stimuli for deeper processing, resulting in a stronger

665 percept and corresponding neural representation. However, here we show that the way

666 that one attends to a sequence of tones can affect how they are grouped into larger

667 objects, not only the strength of their relative perceptual and neural representations.

669 **Summary**

671 Auditory bistability offers a powerful means of understanding how cognitive states,

672 such as listening goals, attention, and prior knowledge, influence perception, while

673 controlling for stimulus differences. Linking subjective reports with neural measures

674 on a trial-by-trial basis allows us to tap into low-level processes, as opposed to post-

675 perceptual decisions. This method identifies signatures of perceptual experience in

676 auditory cortex to demonstrate that attention can go beyond enhancing the

677 representation of a subset of sounds and allow listeners to intentionally alter the

678 number of distinct objects heard to make up the auditory scene.

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Legends

Table 1. Statistics for effects of intention on phase durations (compared to the

Neutral condition)

Figure 1. Stimulus parameters and percept reporting

(**A**) Two triplets of a stimulus sequence consisting of high (H) and low (L) tones with

a frequency separation (Δf) of 4 or 6 semitones. The H tone frequency was 1000 Hz

for soundbooth testing and 1017 Hz for testing with electro-/magneto-

encephalography.

(**B**) Illustrative changes in perceptual organization with corresponding button press

reports. During integration (blue), H and L tones are perceived as belonging to a

single pattern, whereas during segregation (green) they form two separate perceptual

streams. Perception typically alternates every few seconds after a longer initial

integrated phase.

Figure 2. Behavioral analyses

Effects of frequency separation (Δf) and task on (**A**) the percentage of time reporting

segregation, (**B**) the duration of initial integrated phases, (**C**) the duration of

subsequent integrated phases, and (**D**) the duration of segregated phases. Phase

durations are plotted on a log scale. Black squares: listen neutrally, blue triangles:

attempt integration, green crosses: attempt segregation by attending to high tones,

green circles: attempt segregation by attending to low tones. Error bars: 95% within-

participants confidence intervals.

Figure 3. Univariate neural analyses

(**A**) Group timecourse (mean and 95% within-participants confidence intervals) of

neural activity for integrated (blue) and segregated (green) reports in the Neutral

condition, across frequency separations. Each participant's non-artefactual

independent component with the strongest evoked response is included. The timing of

each tone in the triplet is indicated below the plot.

(**B**) Mean and 95% within-participants confidence interval of the reconstructed source

locations for the components from Figure 3A. Sources are combined after projection

to a single hemisphere in a template brain, with coordinates shown in MNI space. The

mean location lies in auditory cortex in the vicinity of posteromedial Heschl's gyrus.

(**C**) t-values for the Neutral Segregated minus Integrated group difference wave,

across frequency separations. Dashed red lines indicate the critical t-values at $p=.05$,

and the shaded red area represents the largest supra-threshold cluster.

(**D**) Differences in neural activity averaged over the time window of interest for

Neutral Segregated minus Integrated (left), Attempt Segregation minus Attempt

Integration (middle), and Attend High minus Attend Low (right), across frequency

separations. Filled circles correspond to individual participants, with mean and 95%

confidence intervals shown in red. The orange circle represents a single participant

also highlighted in Figures 4B, 4C, and 4D, for comparison of results across

univariate and multivariate approaches.

Figure 4. Multivariate neural analyses

(**A**) Schematic illustration of the classification approach. Linear Support Vector

Machines (SVMs) are trained for each participant and frequency separation in the

Neutral condition (left panel) to find the hyperplane (dashed line) that optimally

separates epochs reported as integrated (blue circles) and segregated (green circles).

The SVMs are then applied to epochs (white circles) in the Attempt Integration

(middle panel) and Attempt Segregation (right panel) conditions.

(**B**) Directed feature weights for classification in the Neutral condition, across

frequency separations. A positive weight at a given timepoint reflects that a more

positive neural response contributes to a segregated classification. The mean across

the group is plotted in red with 95% confidence intervals in pink. One peak in the

mean trace lies in the significant 212-256 ms window from the univariate analysis.

However, classification can make use of different features (timepoints) for different

participants. The orange trace corresponds to one participant whose neural activity is

dissimilar to the group mean (both for feature weights plotted here, and raw activity in

the 212-256 window shown in Figure 3D, left) and whose data did not contribute to

the univariate effect of intention (Figure 3D, middle). Perception can nonetheless be

decoded for this participant (Figure 4C), contributing to the multivariate effect of

intention (Figure 4D, left). The timing of each tone in the triplet is indicated below the

plot.

(**C**) Classification accuracy for Segregated versus Integrated epochs in the Neutral

condition, across frequency separations. Filled circles correspond to individual

participants, with mean and 95% confidence intervals shown in red. The orange circle

represents a single participant also highlighted in Figures 4B, 4C, and 4D, for

comparison of results across univariate and multivariate approaches, as described

above. Chance classification accuracy is at 50% (green dashed line).

(**D**) Differences in percentage of epochs classified as segregated for Attempt

Segregation minus Attempt Integration (left), and Attend High minus Attend Low

(right), across frequency separations. Filled circles correspond to individual

participants, with mean and 95% confidence intervals shown in red. The orange circle

represents a single participant also highlighted in Figures 4B, 4C, and 4D, for

comparison of results across univariate and multivariate approaches.

Figure 1. Stimulus parameters and percept reporting

A

B

Figure 2. Behavioral analyses

Listening instruction:

■ Neutral ▲ Attempt Integration ✖ Attempt Segregation (Attend High) ● Attempt Segregation (Attend Low)

Figure 3. Univariate neural analyses

Figure 4. Multivariate neural analyses