Evidence for neural rhythms embedded within binocular rivalry

Oakyoon Cha[a,1] and Randolph Blake[a,1]

[a]Department of Psychology, Vanderbilt University, Nashville, TN 37240

Evidence for perceptual periodicity emerges from studies showing periodic fluctuations in visual perception and decision making that are accompanied by neural oscillations in brain activity. We have uncovered signs of periodicity in the time course of binocular rivalry, a widely studied form of multistable perception. This was done by analyzing time series data contained in an unusually large dataset of rivalry state durations associated with states of exclusive monocular dominance and states of mixed perception during transitions between exclusive dominance. Identifiable within the varying durations of dynamic mixed perception are rhythmic clusters of durations whose incidence falls within the frequency band associated with oscillations in neural activity accompanying periodicity in perceptual judgments. Endogenous neural oscillations appear to be especially impactful when perception is unusually confounding.

neural rhythms | multistable perception | binocular rivalry

Perceptual experience seems to unfold seamlessly, but this belies the evidence that perception comprises discrete epochs in which perceptual responsiveness varies periodically over time (1, 2). The notion of discrete, oscillatory fluctuations in perceptual responsiveness also emerges from studies showing neuronal response modulations in brain activity measured using electroencephalography (EEG) that match fluctuations in perceptual responsiveness (3–5).

It is easy to imagine how oscillatory fluctuations in endogenous neural activity could interact with appropriately aligned pulses of neural activity evoked by discrete sensory stimulation. But recent results suggest that discrete sensory stimulation is not a prerequisite for producing neural signatures of oscillatory fluctuations. Even during prolonged, unchanging visual stimulation, indirect evidence for an influence of endogenous brain rhythms emerges. Thus, for example, neural activity measured during perception of bistable stimuli carries subtle but reliable signatures of periodicity in the EEG activity associated with visual stimuli provoking bistability (6–8). These EEG results reveal the influence of endogenous, oscillatory neural modulation embedded within prolonged, exogenously generated sensory neural signals that culminate in competing perceptual interpretations (9).

Is it feasible to see telltale signs of periodicity within the records of fluctuating bistable perception itself, not just in the concomitant EEG signals? While simple in principle, the practical challenge involves extracting a signature of oscillations in perceptual dominance within time series that are characteristically stochastic (10–14). In principle this should be possible, just as it is feasible to uncover weak stimulus-evoked activity from EEG recordings given a sufficient number of discrete instances of signal within noise.

An earlier study in our laboratory (15) produced a remarkably large binocular rivalry (BR) dataset collected from 16 participants tested over 15 sessions each consisting of 20 blocks of measurements of BR, with each block lasting at least 60 s. This produced an average of 8,729 individual BR state durations for each person (range 4,741–13,854, excluding durations briefer than 500 ms). This large sample afforded the opportunity to parcel state durations into sufficiently narrow time bins that we could extract frequency modulations in duration incidence within the range associated with the EEG measures described above.

This dataset comprised durations for 2 unique BR states, exclusive dominance and mixtures. During exclusive states, observers were experiencing complete dominance of the stimulus viewed by one eye or the other; during mixture states, observers were experiencing bits and pieces of both eyes' stimuli, typically in a dynamic patchwork-like appearance. Mixture states, when they occur, are sandwiched between states of exclusive dominance. According to conventional models of BR, mixture states reflect relatively equivalent levels of neural activity within separate pools of neurons competing to achieve a dominating level of activity sufficient to promote exclusive perception of one eye's stimulus (16). If this view is correct, a reasonable prediction is that durations of mixture, compared with durations of exclusive dominance, would reveal robust frequency modulations associated with unresolved dominance states during which perceptual judgment is confounded. Can we discern evidence for the existence of such modulations in the time series of BR state durations?

To reveal potential traces of frequency modulations embedded in BR state durations, we removed nonrhythmic components from transition probability density histograms by subtracting the best-fitting Gamma distribution (Fig. 1 A–D). These residual variances were then windowed and transformed into a temporal power spectrum (Fig. 1E). We used durations falling within a time window spanning 1 s centered on the median of the fitted Gamma distribution because it provides sufficient frequency resolution to resolve 1-Hz peaks in the temporal power spectrum (analysis code, figures, and data published at https://osf.io/jc4sr) (17). This dataset was collected using a keyboard whose 62.5-Hz polling rate created an artifactual peak at 12.5 Hz. We thus limited the frequency band of interest to 4 to 10 Hz, a range encompassing the frequencies of neural rhythms found in the EEG studies. Data were analyzed on an individual-by-individual basis and then averaged within theta and alpha bands, knowing that peak frequencies vary among individuals (18).

The average power of periodic duration episodes within that frequency band was indeed stronger within the mixture durations relative to the average power within the exclusive dominance durations [$t(15) = 4.011$, $P < 0.01$, Bayes factor $(BF)_{10} = 34.36$, Fig. 1E]. We made no a priori predictions about rhythmic activity in other frequency bands (e.g., beta and gamma), but we nonetheless found evidence that the differences are more conspicuous in the 4- to 10-Hz range compared with the 15- to 50-Hz range [$F(1, 15) = 6.112$, $P = 0.026$, $BF_{inclusion} = 1.333$]. To verify that this difference arises from the temporal structure of residual variance, we shuffled the residual variance histogram values within the 1-s window and repeated the analysis. The shuffled data
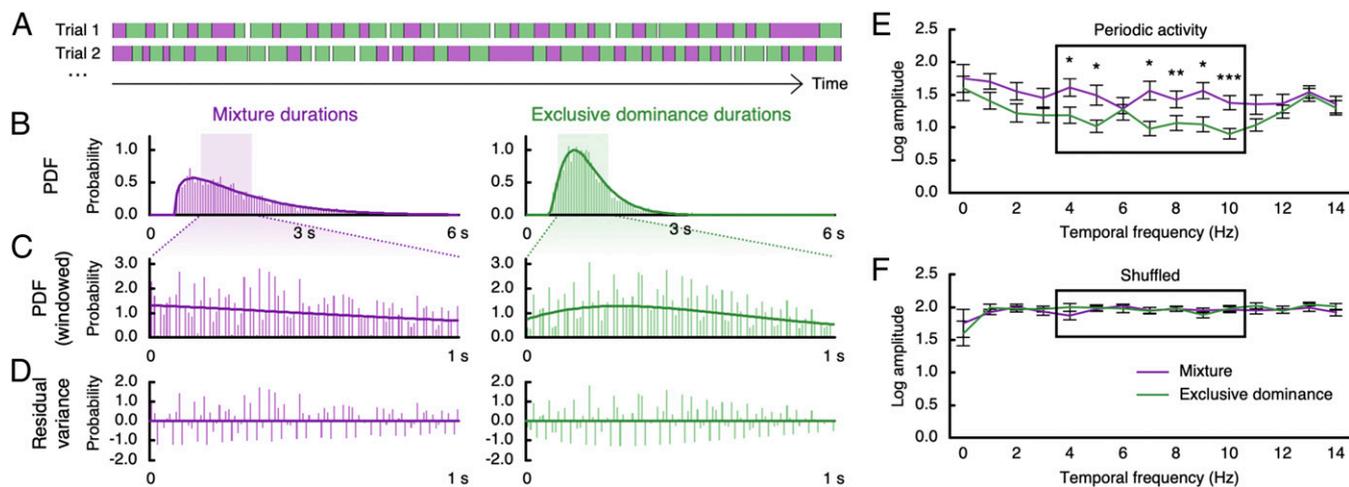
Fig. 1. Analysis steps, S01 as exemplar. Complete data are available at https://osf.io/jc4sr. (*A*) Time series for 2 of the 300 60-s trials. Successive rival states are denoted by colors: Exclusive dominance (green) and mixtures (violet). Durations under 500 ms (white) were excluded in the analysis. (*B*) All durations were fitted to cumulative Gamma distributions separately for mixture and exclusive dominance states. Line graphs show fitted Gamma distributions along with transition probability density histograms (50-ms bins, for presentation purposes). Shaded rectangles demarcate a 1-s time window centered on the median of the probability density function (PDF). (*C*) PDFs and histograms (10-ms bins, for analysis) were windowed and normalized so that the area under the PDF within the 1-s window equals 1. (*D*) PDFs were subtracted from the histograms to derive residual variance for each 10-ms bin, and these residuals were transformed into temporal power spectra (cf. ref. 8). (*E*) Average temporal power spectra of mixed and exclusive dominance durations (*n* = 16 participants). (*F*) Average temporal power spectra with temporal structure disrupted by shuffling residual variance histogram values within the 1-s window. For both *E* and *F*, error bars indicate SEs of means, and asterisks indicate significance from paired-samples *t* tests at each frequency (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

showed no evidence of differential periodic activity [$t(15) = -0.174$, $P = 0.864$, $BF_{10} = 0.259$, Fig. 1*F*], and ANOVA revealed a significant interaction between temporal structure (normal vs. shuffled) and dominance states (mixture vs. exclusive) [$F(1, 15) = 19.81$, $P < 0.001$, $BF_{inclusion} = 48.53$]. This interaction is comparably strong in 2 other time windows, i.e., the 25% point [$F(1,15) = 11.203$, $P = 0.004$, $BF_{inclusion} = 8.823$] and the 75% point [$F(1, 15) = 39.11$, $P < 0.001$, $BF_{inclusion} = 333.27$].

So mixture states indeed contain prominent, detectable periodic modulations in their likelihood of transitioning into stable states of exclusive dominance. Moreover, these rhythmic frequencies embedded in mixture-state durations resemble the dominant frequencies of modulation emerging from single-unit and EEG studies (i.e., theta and alpha bands).

This is not to say that rhythmic neural modulations are not present during states of exclusive dominance. After all, we know that periodic modulations are discernible in the electrical signals

recorded from the scalp during prolonged episodes of BR. Evidently, however, the impacts of those rhythms on duration states for mixtures are significantly greater compared with the robust neural events that govern durations of exclusive dominance, events thought to be governed by neural spiking adaptation (19), internal noise (20), collinear facilitation (21), and top–down attention (22, 23). It is ironic that during multistable perception the visual concomitants of the brain's rhythms become most salient during periods when perception is most confusing and, thus, the competition between unequivocal perceptual interpretations is most fierce (cf. ref. 24). In this respect, mixture states—an underappreciated ingredient in BR—provide a unique window into the rhythms of BR.

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