Beta oscillations correlate with the probability of perceiving rivalrous visual stimuli

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Under continuous lighting, moving stimuli such as ceiling fans and car wheels can sporadically appear to move in the reverse direction—this phenomenon is known as illusory motion reversal (IMR). We have previously suggested that IMR results from the spurious activation of motion detectors tuned for the opposite direction of motion, leading to a rivalry between two possible motion percepts. To determine if this hypothesis is supported by evidence from electrophysiology, we used EEG to directly compare neural signatures in IMR and binocular rivalry (BR), a well-studied form of rivalry. We find that both IMR and BR show large changes in power in the beta range (14–30 Hz) at the time of a perceptual switch. More importantly, during a stable perception, beta power correlates with the probability of a perception. Specifically, beta power associated with veridical motion perception (experienced the majority of the time) is higher than the power during illusory motion perception (experienced a minority of the time). The BR percepts, each 50% probable, are associated with an intermediate beta amplitude. We propose that the amplitude of synchronized beta activity reflects the size of currently active neural coalitions, with less likely percepts associated with smaller coalitions.

Keywords: illusory motion reversal, binocular rivalry, beta oscillation, neural coalitions

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Introduction

During illusory motion reversal (IMR), a continuously moving object is perceived as alternately moving in its veridical direction and in the opposite direction even under continuous illumination (Purves, Paydarfar, & Andrews, 1996; Schouten, 1967). The object is perceived in the veridical direction of motion for the majority of the viewing time and in the opposite motion direction for a smaller but noteworthy viewing time (typically 5–25%; Kline, Holcombe, & Eagleman, 2004; Kline & Eagleman, 2008; VanRullen, 2007).

Kline et al. (2004) proposed that this alternation between opposite percepts is the result of competition within the motion detection system. Specifically, motion perception is thought to arise from Reichardt-like motion detectors (Adelson & Bergen, 1985; van Santen & Sperling, 1985), which, in some cases, can be spuriously activated by motion in the opposite direction (Kline et al., 2004). Normally, the competition is won by the group of detectors encoding the veridical direction, but during a prolonged presentation of the stimulus, spuriously activated motion detectors coding for the opposite direction may dominate and hence control perception (Kline et al., 2004; Kline & Eagleman, 2008). In other words, IMR is caused by rivalry between motion detectors that compete for visual dominance, and the alternation of their dominance accounts for the alternations in the perceived motion direction.

The hypothesis that IMR is a form of rivalry is supported by the observation that the distribution of durations of veridical or illusory motion perception can usually be fit by a gamma distribution (Kline et al., 2004), a signature of other forms of multistable perception such as binocular rivalry (BR; Leopold & Logothetis, 1999). BR is an emblematic case of bistable perception in which two different images are shown, one to each eye, and the images compete over time for perceptual dominance (Blake & Logothetis, 2002; Eagleman, 2001). There is,

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however, a crucial difference between binocular rivalry (BR) and IMR that we wish to exploit in this study: in the typical experimental setting of BR, the competing percepts alternate with approximately equal probabilities, whereas during continuous motion, the veridical direction is perceived for a longer time than the illusory direction. We hypothesize that this difference may be key for detecting the neural signature of these two effects.

We here set out to determine which EEG characteristics are shared by IMR and BR, and how they might differ based on a stimulus' probability of being dominant (i.e., the one that is perceived). Previously, VanRullen, Reddy, and Koch (2006) found that the perception of the veridical motion direction is associated with a peak in the EEG signal at 13 Hz. Unfortunately, their analysis was not sensitive to transient changes because they applied a Fourier transform over the entire time series. Further, there was no comparison to other forms of rivalry.

In this study, we apply wavelet analysis to the EEG signal around perceptual switches in IMR and BR and individuate the frequency bands that correlate with the percepts in these two forms of visual rivalry. A motor control condition allows us to distinguish physiological changes caused by the motor act used to report the perceptual switch.

Methods

Experimental design

Ten healthy adults participated in the experiment, after giving written, informed consent, following an Institutional Review Board approved protocol in accordance with the Declaration of Helsinki. One of them was an author (DME) while the others were naive to the purpose of the experiment. Participants sat comfortably in an electrically shielded, sound-attenuated room in front of a computer monitor with a refresh rate of 100 Hz. Monitors with high refresh rates emulate the IMR phenomenon observed under continuous illumination, and they do not interfere with the illusion (Kline & Eagleman, 2008; Simpson, Shahani, & Manahilov, 2005; VanRullen, Reddy, & Koch, 2005).

Throughout the experiment, the EEG signal from the scalp was recorded on a 128-channel EGI system (Electrical Geodesics, Eugene, OR) sampled at 250 Hz, referenced to the vertex with 0.1–100 Hz analog band-pass filtering before conversion to digital for offline analysis.

In two 10-min blocks, participants watched unidirectional motion, while reporting the perceived direction of motion (Figure 1A). A single, continuous direction of motion was assigned randomly for each subject and did not change throughout the entire recording session; direction was counterbalanced across participants. For one subject, one of the two blocks was discarded because of machine failure. The stimulus consisted of periodic black dots moving horizontally at a constant speed of 26°/s (temporal frequency: 8.4 Hz; spatial frequency: 3.1°/cycle, approximately eight dots were visible at all times; entire stimulus subtended 23.4° visual angle). The left and right edges of the stimulus faded smoothly to the white background so that the dots did not appear and disappear abruptly. Participants were instructed to maintain fixation upon a red point that was centered 2° below the stimulus. They reported the perceived direction of motion by holding down one of two keys, corresponding to leftward and rightward motions.

In a separate block, participants viewed a stimulus that elicited binocular rivalry. The stimulus consisted of overlapping, perpendicular sinusoidal gratings (one red and one blue, with isoluminance of the two colors established by heterochromatic flicker fusion). Participants wore color-filtering lenses—one red and one blue—so that each eye was presented with one of the two gratings. Participants fixated on a 1° white circle in the center of the stimulus and reported the perceived grating orientation by holding down one of two keys for the duration of the percept (Figure 1B).

Following the two blocks of motion viewing and one block of binocular rivalry, participants performed a motor control task in which they pressed and held the two keys alternately at times of their own choosing (Figure 1C). During this task, they viewed a blank white screen.

Behavioral analysis

To test for the previously reported similarity between illusory motion reversal and binocular rivalry (Kline et al., 2004), we quantified the distribution of dominance durations for the veridical motion perception, illusory motion perception, binocular rivalry, and the motor control condition. For all the participants, dominance durations were binned to form an empirical probability density distribution, and the parameters of the best-fit theoretical gamma distribution were estimated with $\alpha = (\bar{x}/s)^2$ and $\beta = s^2/\bar{x}$ (where $\bar{x}$ is the mean and s is the standard deviation). Significance was tested using a Kolmogorov–Smirnov goodness-of-fit test ($\alpha = 0.05$).

EEG analysis

To analyze only real and stable perceptual alternations, we discarded key presses that were identical to the preceding key press (i.e., when the depressed key was released but then immediately redepressed) or when the interval between key presses was less than 1 s. These exclusion criteria were based upon subject reports of moments in which they felt they had "made a mistake."

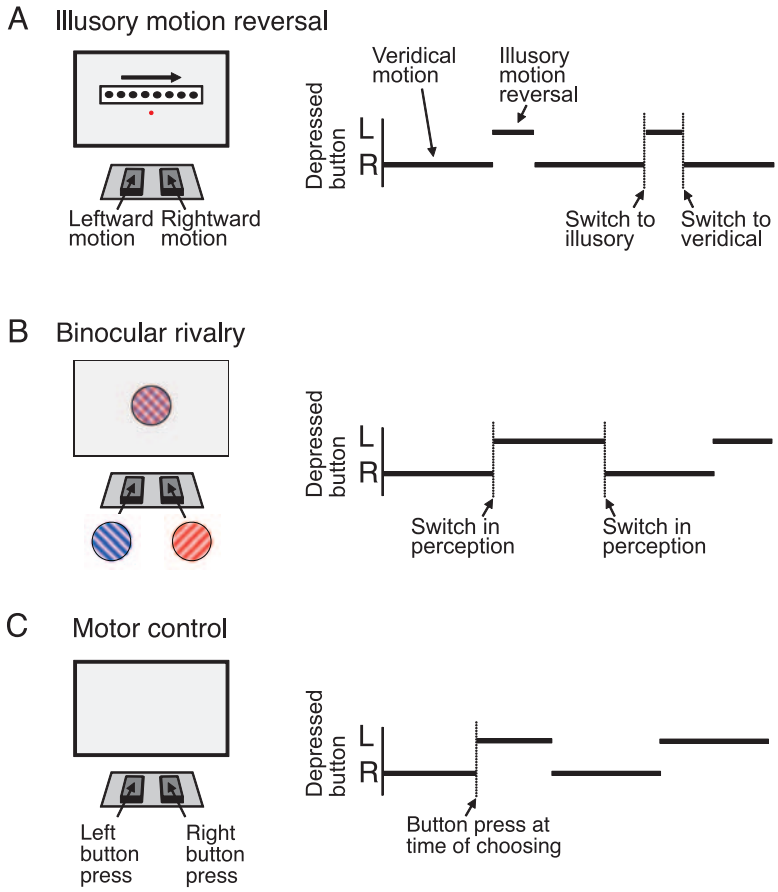


Figure 1. Illusory motion reversal (IMR) was compared with binocular rivalry (BR) and a motor control condition. (A) Participants watched for two 10-min sessions a series of dots moving in a constant direction and reported which direction was perceived. For half of the participants, the actual direction of motion was mirrored. Analysis was conducted separately for the switch into illusory and into veridical direction perception. (B) During BR, participants viewed through color-filtered glasses two superimposed incongruous gratings and reported which one of the two dominated perception. (C) In motor control, participants were asked to press the buttons at times of their choosing.

EEG data were analyzed using FieldTrip software package (http://www.ru.nl/neuroimaging/fieldtrip), a toolbox developed for MATLAB (MathWorks, Natick, MA). A notch filter at 60 Hz was applied to cancel power-line noise. For one participant, noise contamination in other frequencies was so large that data had to be discarded and the analysis was then conducted on the remaining nine participants. Eye movement and muscle-related components were identified by independent component analysis, and these artifactual components were removed from the data (Jung et al., 2000). EEG epochs were analyzed in a window of ±2000 ms around the key press and then checked again for possible eye-related artifacts by visual inspection. In this way, for the two blocks of motion viewing (Figure 1A), roughly half of the key switches indicated a transition into the perceived illusory motion and half a transition into the perceived veridical motion, although total viewing time for the two conditions were different. When analyzing binocular rivalry (Figure 1B), we compared transitions between the red-rightward percept and the blue-leftward percepts. The trials of the motor control condition were combined (i.e., from left button to right, or from right to left) as we expected no difference between them. Oscillatory activity between 4 and 55 Hz was computed using a wavelet-based time-frequency analysis. The signal from each trial was convolved with complex Morlet wavelets, belonging to a wavelet family with a constant ratio f_0/σ_f equal to 5 (Tallon-Baudry, Bertrand, Delpuech, & Permier, 1997). This parameter defines a wavelet duration of 398 ms at 4 Hz and 29 ms at 55 Hz as extreme values. The power of the oscillatory activity was then averaged across the 124 channels covering the whole scalp as there was no *a priori* hypothesis about the location of the activity. Power was computed for the classic frequency bands (theta, 4–7 Hz; alpha, 8–13 Hz; beta, 14–30 Hz; and gamma, 31–55 Hz, see Nunez & Srinivasan, 2006).

A non-parametric randomization clustering approach (Maris & Oostenveld, 2007) was applied to control for multiple comparisons. After computing the *t*-statistic for each time point in the data, the algorithm clusters together those significant data points ($p < 0.05$, two-tailed) that are

temporally adjacent. In this way, it creates clusters characterized by a test statistic defined as the sum of the t-values of its component data points. For the cluster with the largest test statistic, the algorithm computes a surrogate Monte Carlo distribution of the test statistic by randomly reassigning the data points to the two conditions of interest. This reference distribution is then used to estimate the p-value of the test statistics of all the clusters. Data points belonging to clusters with p-values <0.05 are thus considered significant after controlling for multiple comparisons.

Predicting perceived motion direction from EEG data

To determine if oscillatory activity correlates with the perception of veridical motion (see Results section, below), we used the spectral power changes to infer whether the key press reflected a transition into the veridical or into illusory perceived motion. We thus compared the changes in power before and after the key press. In this way, the average power between −2000 and −500 ms was compared with the average power between +500 and +2000 ms. If the beta power decreased in a given trial, the algorithm classified the trial as a transition into illusory and, if it increased, as a transition into veridical motion perception. Then, the classification obtained with this method was compared with the actual responses participants gave. The percentage of correct predictions was calculated on all the 17 blocks (two per participants, excluding one block discarded for machine failure) and the predictive power was tested using a Student's t-test over the 17 blocks with an expected mean of 50% (in the case all the predictions were random).

Results

We analyzed EEG activity when participants experienced switches between perceived directions of motion (Figure 1A), between alternating percepts in binocular rivalry (Figure 1B), and during button presses not associated with perceptual switches (Figure 1C). Based on the hypothesis that IMR is a form of rivalry, IMR and BR were expected to show similar characteristics, which would not occur during the control (button press alone) condition.

Behavioral analysis

First, to ensure that the dominance periods conformed to those reported previously (Kline et al., 2004), a Kolmogorov–Smirnov test was used to test whether the distribution of dominance durations for both IMR and binocular rivalry followed gamma distributions (see Methods section). The gamma distribution was a good fit ($p > 0.05$) for the veridical motion perception (9 participants out of 10) and for the illusory motion perception (7 participants), in line with our hypothesis that IMR is a form of rivalry (Kline et al., 2004; Kline & Eagleman, 2008). We also replicated the finding that dominance durations in binocular rivalry are usually modeled by a gamma distribution (7 participants, see Leopold & Logothetis, 1999). The motor control condition was well fit only in 4 cases. Participants reported seeing the veridical motion direction more often than the illusory one (81.76% and 18.24% of total viewing time, respectively; $p < 10^{-8}$ with a paired t-test), while the two patterns of BR were equiprobable (50.30% and 49.70%, $p = 0.82$).

EEG analysis

In the comparison between the illusory and veridical switch conditions, oscillatory activity showed a significant modulation in two frequency bands: beta (14–30 Hz) and alpha (8–13 Hz). We will address these individually.

Beta frequency band

Activity in the beta frequency band (14–30 Hz) was similar in both of the rivalrous conditions (IMR and BR) around the time of the perceptual switch (i.e., when neither percept was dominant) but differed when perception stabilized (Figure 2). Specifically, the power in IMR and BR was indistinguishable in the interval −500 ms to +250 ms—that is, when the perception was switching (Figure 2; repeated-measures ANOVA, $F(3,21) = 0.819$, $p = 0.50$). In the motor condition, by contrast, the amount of beta power was significantly higher than both IMR and BR conditions for the same interval (Figure 2E, black line; paired t-test between the motor condition and the mean of the rivalrous conditions, $t(8) = 2.85$, $p < 0.025$).

The critical difference in beta power between IMR and BR emerges when one of the percepts becomes dominant. In the IMR condition, beta power was significantly larger during the veridical than during the illusory perception (Figures 2A, 2B, and 2E; green solid lines, veridical; dashed lines, illusory; time intervals −1200 to −900 ms, $p < 0.005$, and −800 to −700 ms, $p < 0.025$, and +900 to +1250 ms, $p < 0.005$). As can be seen clearly in Figure 2, during the switch from veridical into illusory motion perception, beta power decreases (Figure 2A), while the opposite effect is observed during the switch from illusory to veridical motion perception (Figure 2B). Importantly, in the BR condition, the amplitude remains indistinguishable before and after the fluctuation temporarily caused by the switch (Figures 2C and 2D). A paired t-test to confirm

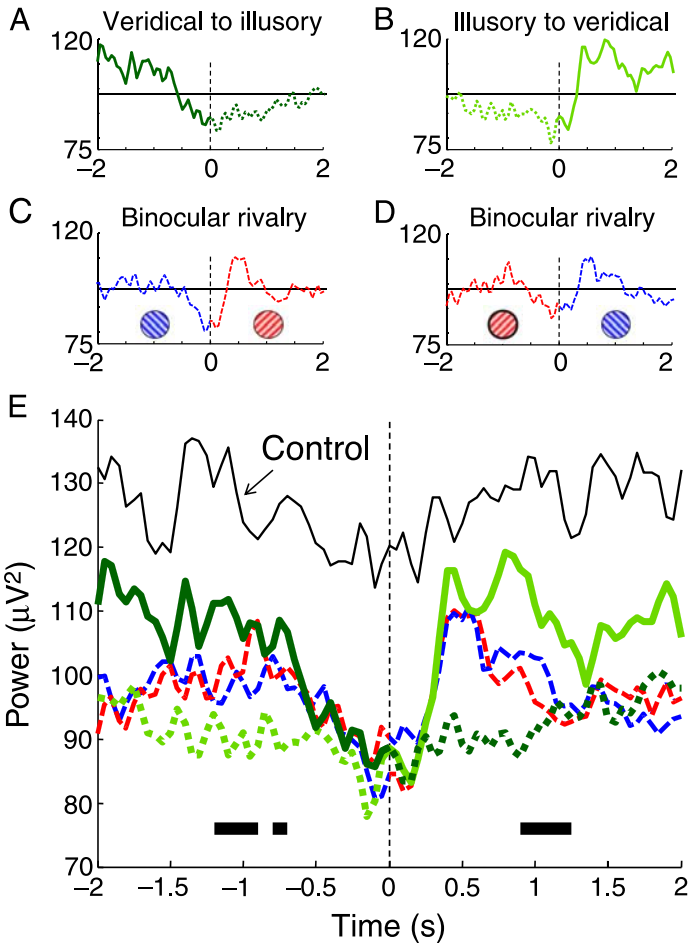


Figure 2. Time course of beta power (14–30 Hz). Averaged EEG activity across all electrodes for (A) transition to illusory motion perception, (B) transition to veridical motion, and (C–D) transitions between the two binocular rivalry percepts. For the motion conditions, solid and dotted lines indicate veridical and illusory perceptions, respectively. Traces are aligned to time 0, the time of the transition between depressed keys. The horizontal line at 97.69 mV^2 represents the mean for all the conditions in this time window. (E) All conditions shown above are combined into one graph. The control condition, in which participants alternated key presses with no visual stimulus, is shown in black. Horizontal bars highlight the periods in which the activity was significantly different between veridical and illusory motions (−1200 to −900 ms, −800 to −700 ms, and +900 to +1250 ms). Note that the conditions were marginally significant ($p < 0.07$) in a larger window that extended from +500 to +1250 ms. The two transitions in the BR conditions were not significantly different at any time point.

this observation between the beta power before and after the switch yielded no significant difference for the BR condition ($t(8) = 0.15$, $p = 0.89$ for Figure 2C and $t(8) = -0.36$, $p = 0.73$ for Figure 2D) while the paired t-test for the IMR condition was significant in both cases ($t(8) = -2.89$, $p < 0.025$ for Figure 2A and $t(8) = 2.75$, $p < 0.025$ for Figure 2B). Below, we will explore the speculation that the probability of a percept correlates with the synchronized activity of underlying neural circuits—that is, more probable percepts are associated with larger neural populations, which, when they dominate, yield a stronger EEG signal.

Predicting perceived motion direction from EEG data

Based on the observation that the beta amplitude correlates with the perceived motion direction, we returned to the raw EEG data and used the beta power before and after each key press to blindly predict the direction of the perceptual switch (see Methods section). Perceptual switches accompanied by beta power decrease (before vs. after switch) were classified as a switch from veridical→illusory perception, and those with beta power increase were classified as illusory→veridical switches. This simple algorithm was able to correctly identify 66.26% of trials for each of the 17 blocks. This percentage was highly significantly different from chance ($t(16) = 5.79$, $p < 10^{-4}$), and in all the blocks except one, the correct classification was above 50%. Although its accuracy is still rather low, this method has a higher success rate than previous presented methods (VanRullen et al., 2006). Generally, this type of analysis is substantially hindered by the poor signal-to-noise ratio of single-trial EEG (Jung et al., 2001), yet in the future more sophisticated algorithms might identify the conscious percept with greater precision.

Alpha frequency band

Activity in the alpha band showed a similar pattern to beta but with a few interesting differences. First, around the time of key press, the oscillatory activity in the motion condition dropped and returned to the initial level after approximately 1 s. However, this drop was not observed in the BR condition (Figure 3).

Second, the amplitude difference between veridical and illusory motion perception was only significant before the key press, specifically in the time interval −2000 to −1800 ms and −1100 to −750 ms ($p < 0.05$ for each time window, Figure 3). Preceding a perceptual switch, veridical motion perception is correlated with larger alpha power than the illusory perception. This result is consistent with VanRullen et al. (2006), in which they report a 13-Hz component associated with veridical motion perception.

Because alpha activity was significantly different before the switch but not after, we wondered whether our time window was not large enough to detect a divergence after the switch. We therefore tried expanding the time window up to +4000 ms and found that alpha activity increases for the veridical condition after ~2500 ms, indicating that alpha activity indeed flips around the perceptual switch, similar to beta activity but with different temporal dynamics. However, these observations must be taken

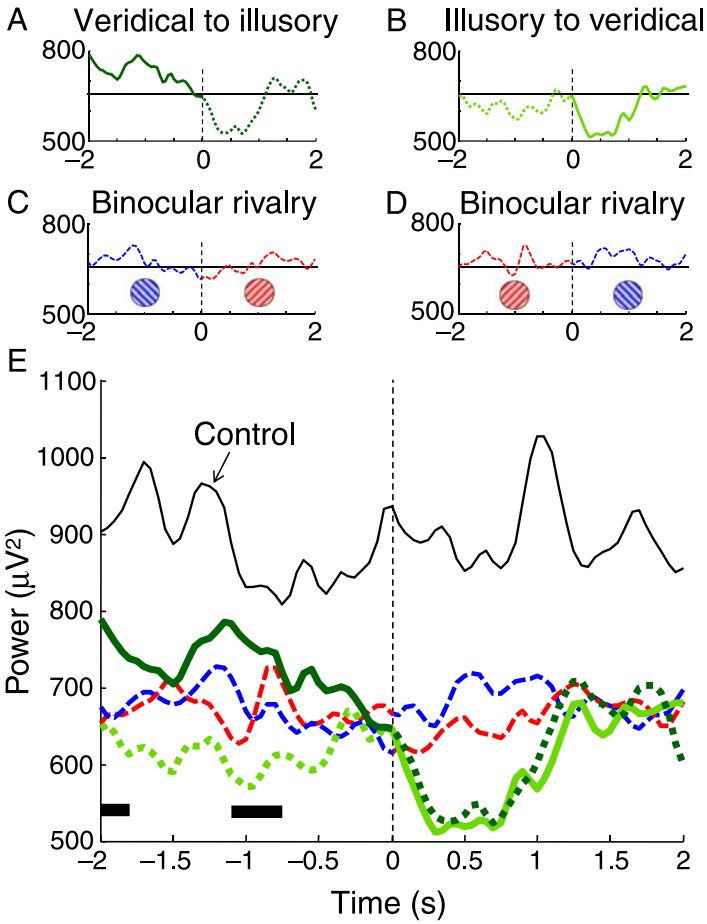


Figure 3. Time course of alpha power (8–13 Hz) averaged across all the electrodes. Color and solid/dashed conventions as in Figure 2. The horizontal line in (A)–(D) indicates the mean of the four conditions at 655.81 mV^2. Before perceptual switches, activity in the alpha frequency band was significantly larger during veridical perception than illusory at −2000 to −1800 ms and −1100 to −750 ms prior to the key press. After perceptual switches, alpha activity did not differ between the two perceptual conditions until ~2500 ms later (not shown). The two transitions during binocular rivalry were not different at any time point.

with caution because the length of this extended time window is larger than the mean perceptual duration of the illusory motion direction.

For completeness, we tried to predict the perceived motion direction based on differences in alpha activity before the switch (specifically, in the window from −2000 to −500 ms). In this case, the algorithm correctly identified, on average, 59% of trials for each of the 17 blocks ($t(16) = 4.55$, $p < 10^{-3}$).

Comparing probability of a percept to oscillatory activity

For the three rivalrous conditions (veridical motion, illusory motion, and binocular rivalry), the magnitudes of alpha and beta oscillatory powers parallel with the percentage of viewing time, which is a measure of the likelihood of perceptual dominance (Figures 4A–4C). During BR, the two percepts have a similar likelihood of being consciously reported, and therefore, the beta power is roughly equal before and after the perceptual switch. In contrast, veridical motion perception is much more likely than illusory perception, and the magnitude of oscillatory power corresponds with each percepts' likelihood.

Speculatively, we suggest that these data can be understood in a framework in which the size of a neural coalition correlates with its probability of dominating (Figure 4D). A percept that has a good deal of neural "support" may be more likely to dominate. When the smaller coalition sporadically dominates, it has fewer synchronized neurons, and thus the power of the synchronized population activity (i.e., the EEG signal) is smaller. If this framework is correct, it implies that the power of the EEG signal can serve as a proxy for the size and/or strength of a neural population that supports a particular percept. This model would also account for the equal amount of power around the time of switch (at least in the beta band): when no percept is dominating, neither coalition is in power and the synchronized activity reaches its lowest level.

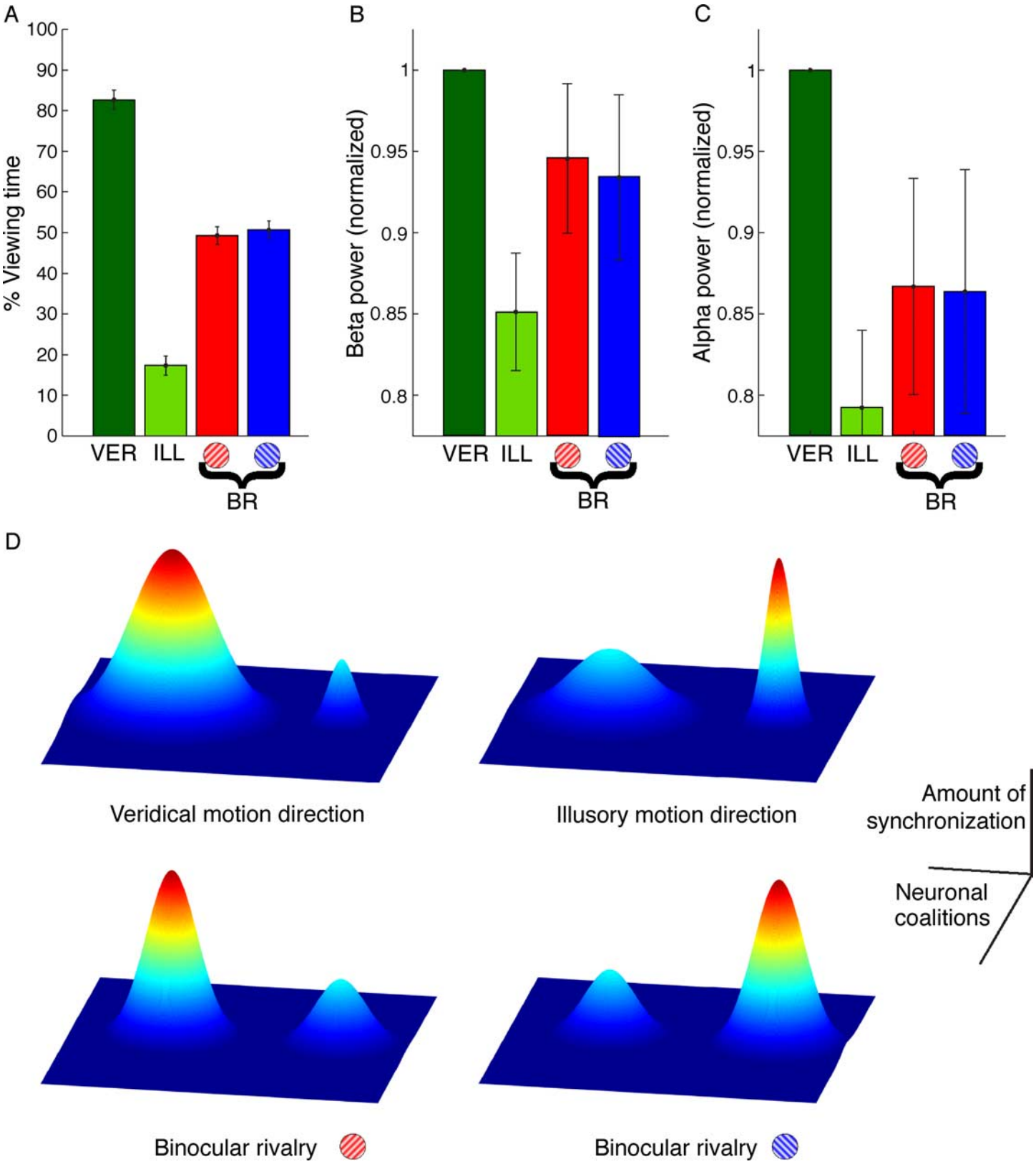
Discussion

Based on psychophysical data, we had previously suggested that the perceptual alternation of motion directions in IMR is the result of the competition between rivaling motion representations (Kline et al., 2004; Kline & Eagleman, 2008). Although biased toward the veridical motion direction, the competition is sporadically and transiently won by detectors coding for the opposite

Figure 4. Oscillatory activity in the alpha and beta bands depends on the likelihood of a percept to be dominant. (A) The probability of perceiving veridical (VER) and illusory (ILL) motion directions and the orientations in BR, measured as percentage of perceptual dominance times. (B) Beta power before the key press (normalized to the veridical condition at −2000 to −500 ms). (C) Alpha power before the key press (normalized to the veridical condition at: −2000 to −500 ms). Error bars represent standard errors of the mean. (D) A hypothetical representation of the competition between neuronal groups of different strengths. A more probable percept (veridical perception) will be represented by a larger neural coalition. In the case of binocular rivalry, the size of the neural coalition for each of the two possible percepts is presumed to be the same. When a coalition wins the competition for perception, its constituent neurons oscillate more synchronously. The measured EEG activity is hypothesized to be proportional to the size of the active neuronal coalition and, consequently, to the likelihood of the perception.

direction. If this hypothesis is correct, we reasoned that investigations into IMR and binocular rivalry (BR) could reveal common underlying mechanisms. In the present experiment, we report changes in synchronized oscillations that correlate with the conscious perception.

It has been hypothesized that conscious perception arises from coalitions of neurons whose activity, when maintained above a critical threshold, represents a percept (Crick & Koch, 2003). The oscillatory activity that maintains such coalitions has been linked to visual



perception and awareness (Crick & Koch, 1990; Engel & Singer, 2001). Extending these hypotheses, we propose that the *amplitude* of these oscillations reflects the effectiveness of the neural coalitions representing the competing percepts—that is, which of two rivaling percepts dominates at any moment (Figure 4D). In other words, the size of the neuronal ensemble that drives the widespread oscillatory activity determines the power of the EEG signal. In the case of motion viewing, more neurons encode the veridical direction than the illusory one, and when the perception is driven by the former, the amount of EEG activity measured at the scalp will be larger. In contrast, equally sized coalitions are responsible for the two equiprobable percepts during BR, resulting in an almost equal level of beta power during the two possible percepts.

Beta frequency band

The following lines of evidence support beta oscillations as an index of visual perception. Changes in beta power between veridical and illusory motion directions are so consistent that it was possible to predict the perceived motion direction on the basis of the difference in synchronized activity with good accuracy. Conversely, during BR, in which the percepts are equiprobable, the average power preceding and following the transition did not significantly change (Figures 4A–4C). Finally, a temporally specific low level in beta activity was present at the time of the key press for the three rivalry conditions but not for the control motor condition. We hypothesize that this lower, unspecific activity is the result of the disengagement of the synchronized activity underlying a stable percept—in other words, there is a transition of coalitions during the switch, meaning that neither population is well synchronized.

Furthermore, capitalizing on the difference between veridical and illusory motion perceptions, we compared the scalp topography of the beta power for the IMR condition (Figure 5). The topographical distribution of the power difference between the two conditions was extremely stable before and after the switch. The scalp topography showed the largest differences over the occipital–parietal areas, which reflects the involvement of neuronal generators located in the extrastriate visual cortex, as reported in neuroimaging studies of visual rivalry (Lumer & Rees, 1999; Tong, Nakayama, Vaughan, & Kanwisher, 1998). This confirms the hypothesis that the amount of synchronization of specific groups of neurons organized in coalitions is responsible for the conscious perception.

If perception is underpinned by distributed neural coalitions (Crick & Koch, 2003), synchronized beta oscillations could represent the mechanism underlying long-range communications in a brain network. This is in contrast to gamma activity, which operates on a smaller spatial scale (Kopell, Ermentrout, Whittington, & Traub, 2000; Sehatpour et al., 2008; von Stein, Rappelsberger, Sarnthein, & Petsche, 1999). Long-range communication in neuronal networks might be necessary to integrate the global neuronal workspace, a collection of areas theorized to be necessary for conscious perception (Baars, 2005; Dehaene & Naccache, 2001). Evidence for a role for the beta frequency in long-range synchronization of brain activity comes from multisensory integration (Senkowski et al., 2007), visual detection tasks that involve sensory, parietal, and motor areas (Brovelli et al., 2004; Classen, Gerloff, Honda, & Hallett, 1998; Donner et al., 2007), and the distributed maintenance of visual objects in short-term

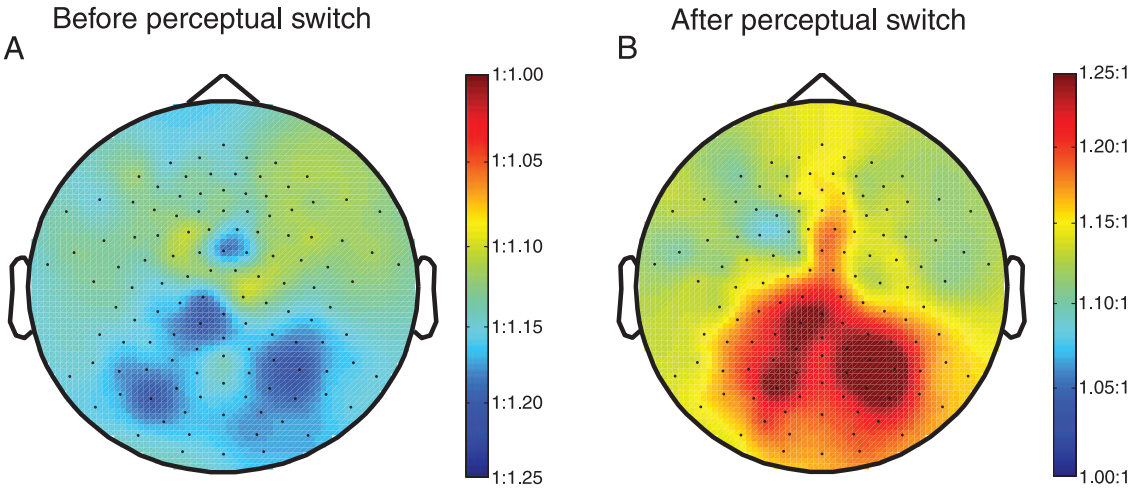


Figure 5. Scalp topography of beta power for the illusory motion condition (A) before the perceptual switch (−2000 to −500 ms) and (B) after the perceptual switch (+500 to +2000 ms). The colors represent the ratio between the transition from veridical to illusory (Figure 2A) and the transition from illusory to veridical (Figure 2B). The similarity between the topographical distributions of the differences in beta power suggests that power changes are due to the modulation of the synchronization of the very same neuronal generators.

memory (Tallon-Baudry, Bertrand, & Fischer, 2001; Tallon-Baudry, Mandon, Freiwald, & Kreiter, 2004).

The importance of long-range communication in bistable perception and, in particular, in IMR has been corroborated by a recent study using repetitive transcranial magnetic stimulation (rTMS; VanRullen, Pascual-Leone, & Battelli, 2008). Disruption through rTMS of the left parietal region (a component of the global neuronal workspace, Dehaene & Naccache, 2001) shortens the time in which the illusory direction was perceived, presumably by weakening the interaction between visual areas and higher level regions.

Alpha frequency band

VanRullen et al. (2006) reported a specific EEG component at 13 Hz associated with motion perception, whose power was significantly lower during illusory perception. This finding is replicated here as a more broadband alpha modulation (short-time wavelet analysis has a lower spectral resolution than the Fourier transform). The power changes around the perceptual switch are also similar in the two experiments, disregarding baseline differences.

Although alpha and beta powers both flip around the time of the switch in motion perception, their temporal variations are not identical, suggesting a decoupling between the information carried by the two frequency bands. Whereas the beta power for illusory and veridical perceptions diverges soon after the perceptual switch, alpha power does so much later. Furthermore, alpha power is not strongly modulated in the BR condition. These findings call into question whether alpha directly correlates with the conscious perception, yet the functional role of this activity remains elusive. Indeed, the literature does not reveal a consensus on the cognitive correlates of the alpha oscillations. Alpha activity has been shown to be modulated by a wide variety of phenomena, including visual attention shifts (Ray & Cole, 1985), short-term memory (Jensen, Gelfand, Kounios, & Lisman, 2002), and performance of mental tasks (Cooper, Burgess, Croft, & Gruzelier, 2006), and has been proposed to underlie both cortical inhibition (Klimesch, Sauseng, & Hanslmayr, 2007; Pfurtscheller, 2003) and top-down neuronal processing (Palva & Palva, 2007). Because of this uncertainty, it is difficult to be certain about the interpretation of the alpha signal in the present experiment.

Conclusions

We have presented evidence for a functional role of synchronized activity during perceptual rivalry. We hypothesize that the amplitude of oscillatory activity (in the alpha and beta bands) is proportional to the likelihood that a rivaling image is consciously perceived. This follows the theoretical proposal that oscillatory activity mediates long-range synchronization maintaining connectivity in a distributed brain network.

As the evidence presented here was limited to two conditions, future research is necessary to confirm this hypothesis. Experimental manipulations that could lend further empirical support to this hypothesis include parametric adjustments of the probabilities of the two percepts, as well as other forms of bistable perception.

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