Alpha band amplification during illusory jitter perception

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Synchronization is thought to have a role in linking disparate components into neural assemblies. However, the particular frequency of the synchronization is generally considered to be incidental to its functional role. Here we report a link between enhanced alpha activations and an illusory jitter of the same frequency. We measured perceived jitter rates and the magnetoencephalography during presentations of a stimulus wherein red squares and superimposed vertical green bars moved together across a black background. The green bars were either darker, equiluminant with, or brighter than the red squares. We established that the illusory jitter rate, robustly seen only in the equiluminant condition, was ~10 Hz. Crucially, neural oscillations around 10 Hz were enhanced in this condition. Surprisingly, ~10 Hz oscillations were also enhanced during illusory jitter perception relative to a moving stimulus that contained physical 10 Hz jitter. This suggests that the enhanced synchronization is associated with illusory jitter generation rather than with jitter perception. Since the stimulus eliciting illusory jitter moves smoothly and rigidly, both the percept and enhanced neural synchrony must be generated within the visual system. Our data therefore indicate a match between the dynamics of synchronous neural activity and the dynamics of a sensory experience offering the intriguing possibility of a common cause.

Keywords: MEG, neural oscillation, alpha band, motion, jitter, illusion

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Introduction

Synchronized neural oscillations have been implicated in a number of functional processes. For instance, they have been implicated in the tagging of neurons that comprise a particular momentary neural assembly (von der Malsburg, 1981), the binding of disparate neuronal representations to generate a unified and coherent percept (Gray & Singer, 1989; Singer & Gray, 1995), as a mechanism by which multiple items might be encoded within a single train of neural activity (Lisman & Idiart, 1995; Llinás, Ribary, Contreras, & Pedroarena, 1998), and in the establishment of effective connectivity between disparate processing units through phase locked activations (Fries, 2005). They have also been considered to reflect the operation of dynamic interactions, such as predictive feedback between different brain regions (Engel, Fries, & Singer, 2001).

According to some of these proposals, the frequency of oscillation should be intimately linked to the temporal dynamics of the hypothesized mechanism. For instance, effective connectivity could be achieved by ensuring that input arrives at the phase at which the receiving cell is most excitable (Fries, 2005). However, while oscillation frequency has been linked to the optimal dynamics for information processing, as of yet the temporal dynamics of neural activations have not been directly related to the dynamics of a perceptual experience.

Here we report data that, we believe, ties a characteristic oscillation frequency to the dynamics of an illusory perceptual experience. When color-defined and luminance-defined borders are moved together, the equiluminant border can appear to jitter at a characteristic frequency (Arnold & Johnston, 2003, 2005). This phenomenon has been described as motion induced spatial conflict (MISC). Surprisingly the perceived jitter rate does not depend on stimulus parameters, such as motion speed

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or the spatial displacement of the different types of moving border (Arnold & Johnston, 2003, 2005). These observations suggest that the illusory jitter might be internally generated, rather than stimulus driven. It was hypothesized that the illusion is a consequence of recurrent neural processes that mediate the integration of motion-based spatial predictions and subsequent spatial processing—a process sometimes experienced as spatial jitter. If correct, this would provide the first evidence for a direct link between the dynamics of neural processing and the dynamics of a perceptual experience.

To test this proposal, we combined psychophysics with magnetoencephalography (MEG) to study neural activity during illusory jitter perception. We report enhanced alpha band neural oscillations during illusory jitter perception relative to control conditions in which illusory jitter is not perceived. Although there was no physical jitter within the stimulus, there was very close agreement between the frequency of the enhanced neural oscillations (~10 Hz) and the frequency of the illusory perceptual experience. Crucially, oscillations during illusory jitter were also enhanced relative to a physical jitter condition, during which illusory jitter was mimicked by the addition of physical jitter to the stimulus. The difference between these two conditions shows that enhanced 10 Hz oscillations during MISC are associated with illusory jitter generation rather than with jitter perception. These results suggest that MISC is generated within the cortex by a dynamic cortical feedback circuit.

General methods

Eleven observers (aged 24–33 years, all male) participated. All were healthy and had normal or corrected-to-normal vision.

Visual stimuli were generated using VSG2/3 (Cambridge Research System, Cambridge) and projected by a digital light processing (DLP) projector (V-1100Z; PLUS, Tokyo, Japan) onto a translucent screen (40 deg × 30 deg) located 140 cm from the observer.

Prior to the experiments, we determined green (CIE 1931: $x = 0.34$, $y = 0.57$) luminance values, for each observer, which were subjectively equiluminant with red (CIE 1931: $x = 0.65$, $y = 0.33$, luminance = 0.87 cd/m^2) by using a minimum motion task (Anstis & Cavanagh, 1983). In the subsequent experiments, we used the average of these (across observers) to define a green luminance level (0.64 cd/m^2) that, perceptually, was approximately equiluminant with red. For ease of description, we refer to conditions in which we have used this value as being either equiluminant or near equiluminant to distinguish them from conditions in which there was a substantial luminance component at otherwise chromatic boundaries. Strictly, our equiluminant conditions would have contained some luminance contrast. However, from previous work (Arnold & Johnston, 2003, 2005), we know that subjects reliably report jitter across a range of red-green luminance differences close to zero.

In total, there were six experimental conditions. In conditions 1–3 (dark, equiluminant and bright conditions, respectively), stimuli consisted of vertical green bars (width 0.4°, height 3.0°) superimposed upon larger red squares (3 × 3°). These patterns moved together, horizontally, across a black background and were centered 3° above and below a central fixation point (Figure 1A). The green bars were either darker than (0.19 cd/m^2 condition 1), near equiluminant with (0.64 cd/m^2, condition 2), or were brighter than (1.33 cd/m^2, condition 3) the larger red squares.

At the start of each stimulus presentation, the pattern was centered 10.5° to the left or right of the central fixation point and then it moved across the display at a speed of 6°/s for 3 seconds. To reduce brain activity evoked by the sudden appearance or disappearance of the stimulus, the stimulus appeared behind a triangular window (see Figure 1A), such that the stimulus initially seemed to grow in height and then to contract.

In condition 4 (parallel condition), the stimulus consisted of a horizontal green bar (width 3°, height 0.4°) superimposed on a larger red square (3 × 3°). The luminance of the green bar was the same as in condition 2 (0.64 cd/m^2) and was near equiluminant with the red square. In this configuration the direction of motion was parallel to the chromatic contours, so movement was only signaled by the relatively large changes in luminance at the boundaries of the stimulus (i.e., from black to green, or from black to red; see Figure 1B).

In condition 5 (isolated condition), a vertical green bar (width 0.4°, height 3.0°) moved across a red background. Again, there was minimal luminance contrast between the red and the green sections of this stimulus. We refer to this as the isolated condition as, although the motion signal was defined by near equiluminant colour contrast, it was not shown in close proximity to moving luminance borders (see Figure 1C).

In condition 6 (real condition), physical jitter was added to the type of stimulus used in condition 1 (a dark green bar superimposed upon larger red square) to mimic illusory jitter perception with a physical stimulus (see Figure 1D). The frequency of real jitter was matched to the frequency of illusory jitter measured for each subject in a preceding psychophysical experiment (see below).

Psychophysical measurements

Conditions 1–5 were assessed in a psychophysical experiment prior to MEG recordings. In this experiment, we obtained an estimate of illusory jitter rate by

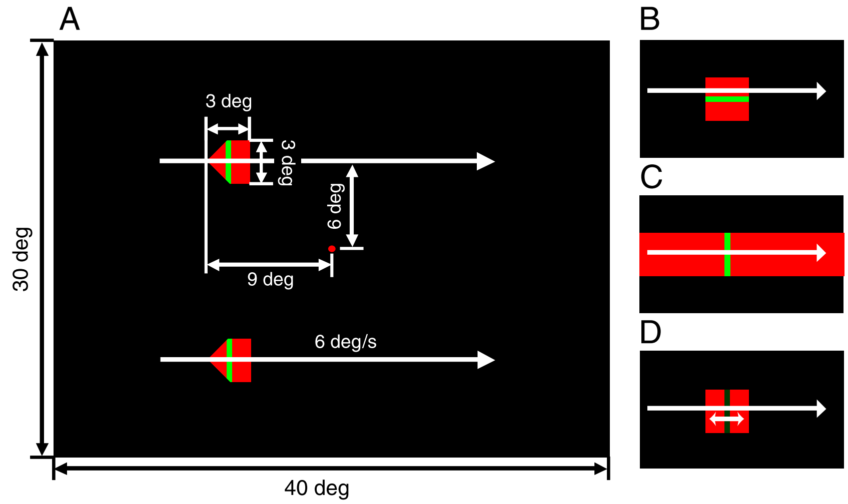

Figure 1. (A–D) Stimulus configurations. (A) Conditions 1–3 (dark, equiluminant and bright conditions, respectively): red squares and superimposed vertical green bars moved together horizontally across a black background. The luminance of the green bars was either darker than (condition 1), near equiluminant with (condition 2), or brighter than (condition 3) the red squares. To reduce brain activity evoked by the sudden appearance or disappearance of the stimulus, the stimulus appeared behind a triangular window. (B) Condition 4 (parallel condition): horizontal green bars superimposed on red squares moved horizontally across a black background. In this configuration, the red-green borders were parallel to the motion direction. (C) Condition 5 (isolated condition): vertical green bars moved horizontally across a red background. (D) Condition 6 (real condition): physical jitter was added to a dark green bar to mimic illusory jitter perception with physical stimulus. In all conditions, the stimuli were presented in both upper and lower visual fields.

having participants match it to physical jitter rates. We used the same apparatus to generate and present visual stimuli during the psychophysical experiments and in the later MEG recordings, although in the case of the MEG study both upper field and lower fields stimuli were identical.

In each condition, test and matching stimuli were presented simultaneously in the lower and upper visual field, respectively. Matching stimuli were similar to the stimuli used in condition 6. After each stimulus presentation, observers were required to indicate if the test stimuli in the lower visual field had appeared to jitter.

If illusory jitter was reported, observers were then required to indicate which appeared faster—the illusory jitter rate or the physical jitter rate. The rate of physical jitter was then adjusted up or down according to the observers response (between the values of 5, 5.2, 5.5, 5.7, 6, 6.3, 6.7, 7.1, 7.5, 8, 8.6, 9.2, 10, 10.9, 12, 13.3, 15, 17.1, and 20 Hz) and then another stimulus was presented. This sequence was repeated until the observer indicated that the rates of illusory and physical jitter seemed to match. The amplitude of physical jitter was 0.1 deg which, subjectively, closely approximated the illusory jitter percept. The five stimulus configurations were presented in a pseudo random order on five occasions each—so the estimates of illusory jitter rate determined for each participant are based on five subjective matches of physical jitter to illusory jitter rates.

MEG recordings and analysis

During MEG recordings, stimuli from each of the six conditions were presented, in a pseudo random order, 100 times each. In all conditions, motion directions of the stimuli in the upper and lower visual fields were the same for 6 subjects and the opposite for 6 subjects (one subject participated in both conditions of the experiment). The directions were randomized across trials for both groups. There was no psychophysical task during the MEG experiment. Both upper and lower fields were identical.

Brain magnetic fields were recorded in a magnetically shielded room using a whole-head MEG system (PQ2440R, Yokogawa, Japan) with 230 axial gradiometers ($\partial Bz/\partial z$) and 70 * 3 vector sensors with one axial ($\partial Bz/\partial z$) and two planar gradiometers ($\partial Bx/\partial z$, $\partial By/\partial z$). Data were sampled at 500 Hz with a 200-Hz low-pass filter and a 0.3-Hz high-pass filter. Fourier analysis was applied to calculate the power spectrum density (in units of fT^2/Hz) for each single trial and for each sensor (frequency resolution was 0.49 Hz). Since we are interested in sustained neural activities during jitter perception, rather than in the onset or offset responses to the stimulus, Fourier analyses were limited to the middle 2 seconds of each stimulus presentation.

In order to determine the neural frequencies associated with illusory jitter perception, we conducted a repeated-measures one-way ANOVA across 6 conditions, for 40 narrow frequency bands. The frequency bands were centered at 2.9, 5.4, 7.8, 10.3,… 98.1 Hz and included 5 frequency bins (1.96 Hz width). For each frequency band, we selected channels whose amplitude was significantly different across conditions, individually for each subject. A one-way ANOVA was applied to the averaged amplitude within each frequency band, comparing each individual's distributions of single trial data for each condition. The channels for which the amplitude showed significant variation across the different stimulus conditions ($p < 0.05$) were selected for further analysis (as per Liu, Harris, & Kanwisher, 2002). For each subject, we then averaged the amplitudes of the selected sensors, for each condition and for each frequency bin.

Distance of the sensors from the sources of alpha modulations, and the orientations of those sources relative to the sensors, can physically amplify or attenuate signals in an idiosyncratic fashion for each observer. Since we are interested in relative change in the power spectrum across our experimental conditions, we analyzed the data under a log transform. The transformed data provided a better fit to the normal distribution.

We analyzed the log-transformed data using a repeated measure ANOVA to determine the frequency bands that showed significant changes with experimental conditions using a correction for multiple comparisons ($\alpha' = 0.05/40$). We then conducted planned comparisons for the frequency bands found by ANOVA. Because we specifically wanted to determine whether the critical equiluminant condition could be separated from all of the other experimental conditions, we compared condition 2 with all other conditions (planned comparisons).

MEG responses were also recorded while subjects closed their eyes (eye-closed condition) for 9 subjects. The measurement lasted for 9 min, and the other measurement parameters were equal to those for the experiments with visual stimuli.

Results

Psychophysical measurements

Illusory jitter was reported in ~70% of trials for the critical equiluminant condition (see Figure 2A). However, it was rarely (if ever) reported in the other stimulus conditions. The rate of illusory jitter, in the equiluminant condition, was matched to a physical jitter frequency of 10.5 Hz (±0.7 Hz; range: 6.2–15.8 Hz). Previous studies by Arnold and Johnston found that subjects matched illusory jitter rates to luminance flicker rates of ~22 Hz (range ~17–26 Hz). We suspect that subjects matched the bright phase of the luminance flicker to the illusory jitter in the previous studies but each change in position in the physical jitter to the illusory jitter here. Thus, in the previous experiments, the matching frequency was roughly double the illusory jitter rate reported in the present study.

MEG recordings

Figure 3A shows frequency spectra averaged across sensors in the frontal, temporoparietal, and occipital regions in the right and left hemispheres, for one of our subjects.

The frequency spectrum of MEG responses in temporoparietal and occipital sensors showed a prominent peak in the alpha band at around 10 Hz (see Figure 3B for the iso-contour map of the alpha power of condition 2). The peak frequency was quite similar for all stimulus conditions (10.2 ± 0.4, 10.3 ± 0.4, 10.1 ± 0.4, 10.2 ± 0.4, 9.8 ± 0.3, and 10.1 ± 0.4 for conditions 1–6, respectively). We found that this frequency matched the psychophysically determined jitter rate (10.5 Hz; $t_{11} = 0.17$, $p = 0.87$).

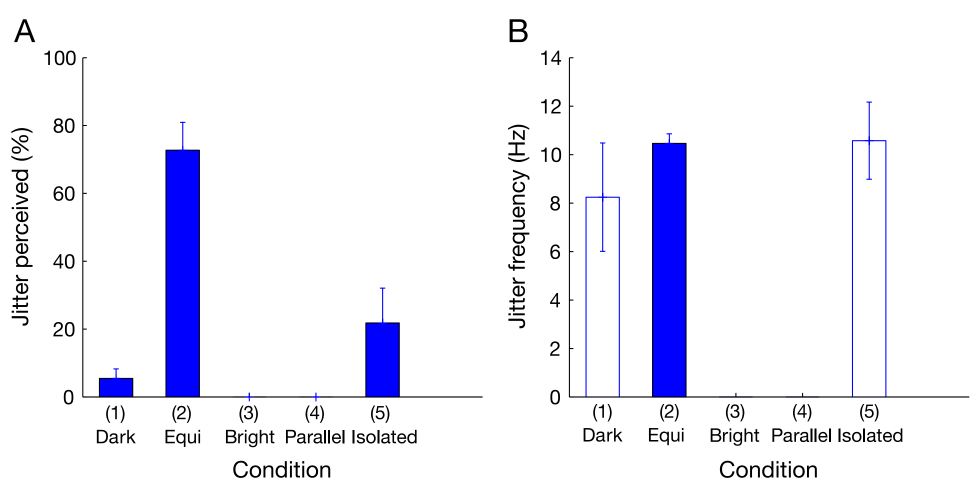

Figure 2. Psychophysical results averaged across all subjects. Error bars indicate ±1 *SEM*. (A) The percentage of trials in which illusory jitter was perceived. Only in the equiluminant condition did subjects consistently perceive the green bars as jittering. (B) The frequency of perceived illusory jitter, measured using a physically jittering stimulus. The perceived frequency of illusory jitter under the equiluminant condition was around 10 Hz.

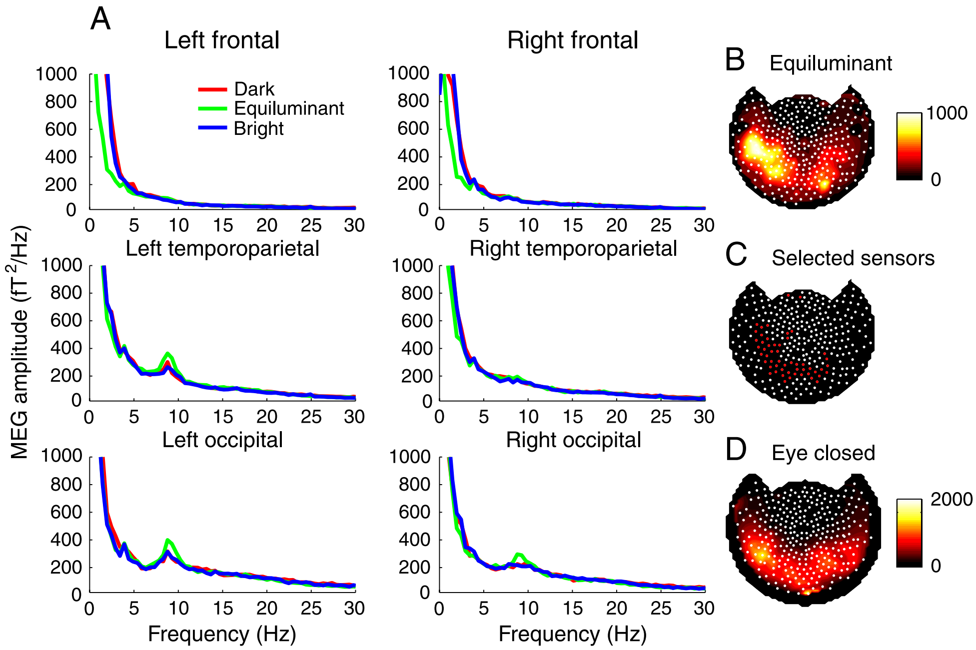

Figure 3. The frequency spectrum and iso-contour map of recorded MEG for one subject. (A) Each panel shows the spectrum averaged across sensors in frontal, temporoparietal, and occipital sensors in left and right hemispheres. The spectrum showed a peak at around 10 Hz, in the alpha band, and the amplitude was largest under the equiluminant condition, in which illusory jitter was perceived. (B) Iso-contour map of 10.3-Hz band amplitude under the isoluminant condition. (C) The location of channels which showed a significant difference across conditions for the 10.3-Hz band and were used for the group analysis. (D) Iso-contour map of alpha band amplitude under the eye-closed condition, which is significantly different from that of the equiluminant condition (B).

To find out which neural frequencies were specifically associated with illusory jitter perception, we conducted one-way ANOVA on log-transformed data for each narrow frequency band. Since the results are not affected by whether the upper and lower stimuli moved in the same or opposite direction, we pooled all subjects. Figure 4A shows the *p*-value of the ANOVA testing the effect of stimulus condition on the amplitude within each frequency band. We found that only the 10.3- and 15.1-Hz bands showed the significant modulation across conditions, indicative of a neural correlate of illusory jitter perception ($F(5,9) = 13.0$, $p < 0.001$, $F(5,9) = 5.2$, $p < 0.001$). The effect at 12.7 Hz was also marginally significant ($F(5,9) = 4.2$, $p = 0.004$). Then we conducted planned comparisons for these frequencies. First, we examined the 10.3-Hz band since this frequency matches the reported rate of illusory jitter.

Planned comparisons between the equiluminant and dark or bright conditions showed that average 10.3 Hz band amplitudes in both the dark ($F(1,9) = 5.0$, $p = 0.03$) and bright ($F(1,9) = 13.4$, $p = 0.003$) conditions were significantly reduced relative to the equiluminant condition. Thus, the presence of illusory jitter was accompanied by a higher MEG amplitude in the alpha band (see Figure 4C).

To exclude the possibility that enhanced alpha band activity during illusory jitter results from viewing the motion of near equiluminant borders *per se,* rather than being related to illusory jitter perception, we measured MEG under the two conditions in which the motion of equiluminant borders does not elicit illusory jitter. MEG recordings (Figure 4C) revealed that alpha band activity under both the parallel ($F(1,9) = 6.0$, $p = 0.02$) and the isolated ($F(1,9) = 54.7$, $p < 0.001$) conditions was reduced relative to the equiluminant condition. Thus, the enhanced alpha band activity in the equiluminant condition must result from the perception of illusory jitter rather than from the motion of equiluminant borders *per se*.

Finally, we tested whether enhanced alpha band activity is related to the generation of illusory jitter or whether it is simply a correlate of jitter perception, by measuring MEG responses under the physical jitter condition, in which real jitter was added (see General methods) to a dark green bar centered in the moving red square (condition 6). The alpha band activity in this condition (Figure 4C) was significantly reduced relative to that during the equiluminant condition ($F(1,9) = 15.6$, $p = 0.002$). This shows that jitter perception *per se* does not enhance alpha band activity and indicates that the enhanced activity is therefore associated with the generation of *illusory* jitter.

Figures 3C and 4D show the sensors selected by ANOVA (see General Methods for details) at 10.3 Hz, for the representative subject and those averaged across all subjects, respectively. These figures again indicate that the

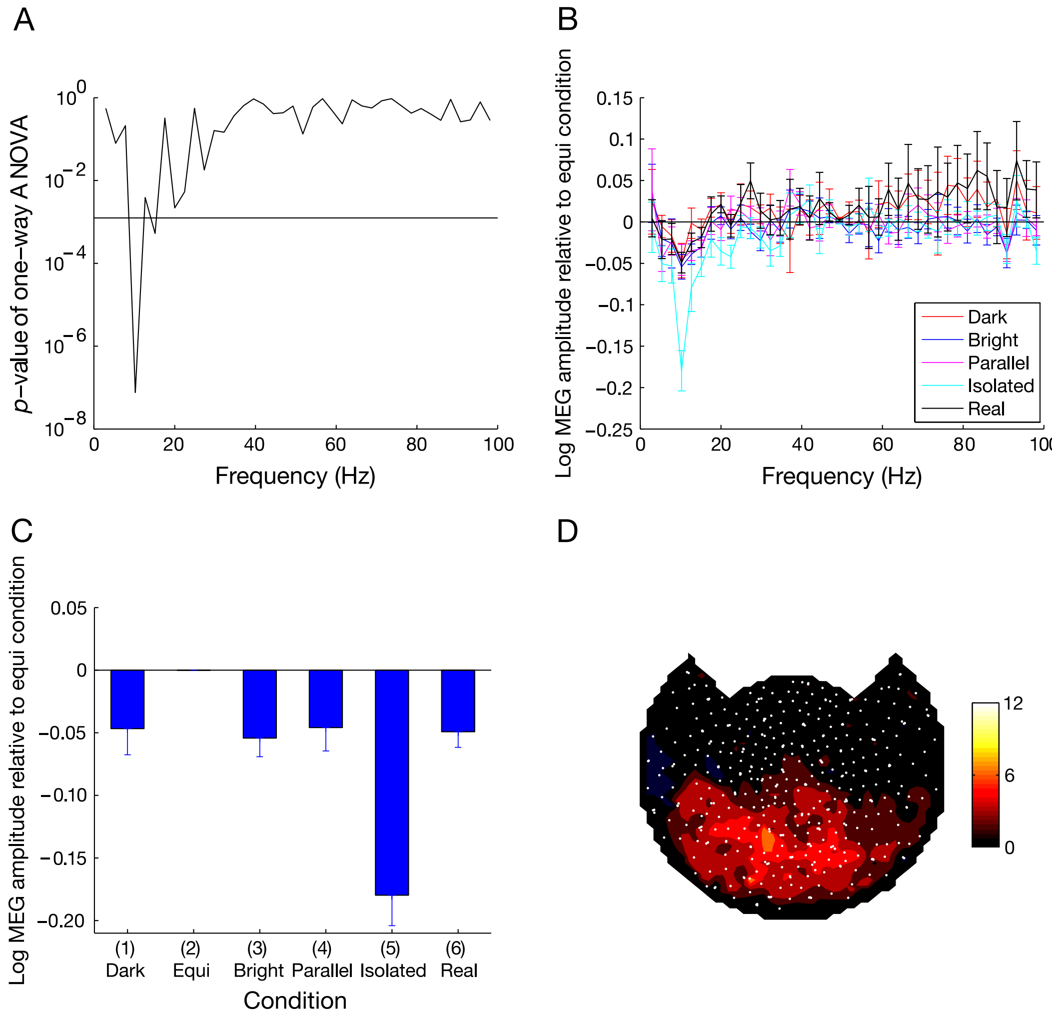

Figure 4. (A) *P*-value of one-way ANOVA for each frequency band. Only 10.3 and 15.1 Hz showed significant effects. Only 10.3 Hz showed significant differences between equiluminance condition. (B) Log of MEG amplitude relative to the equiluminant condition. (C) Comparison of amplitude of 10.3 Hz across conditions. The amplitude under the equiluminant condition is significantly larger than that under all the other conditions. (D) The location of selected sensors for the analysis of 10.3-Hz band, averaged across subjects. The brightness of each sensor indicates the number of subjects with which the sensor was selected.

selected sensors were mainly found in occipital areas. It should be noted that the spatial distribution of the alpha band activity during the equiluminant condition (Figure 3B) was different from that measured during an eye-closed condition (Figure 3D), in which subjects just closed their eyes and relaxed. While the averaged correlation coefficient between the spatial maps associated with the equiluminant condition and the other visual conditions was extremely high (r = 0.988 ± 0.003, r = 0.987 ± 0.003, r = 0.988 ± 0.003, r = 0.959 ± 0.01 and r = 0.990 ± 0.002, respectively), the correlation between the equiluminant condition and the eye-closed condition (r = 0.699 ± 0.067) was significantly lower (paired t tests t_9 = 4.4, p = 0.002; t_9 = 4.3, p = 0.002, t_9 = 4.3, p = 0.002, t_9 = 3.9, p = 0.004, t_9 = 4.4, p = 0.002). This shows that the alpha band activity measured during the visual stimulation conditions can be distinguished from alpha band activity seen in relaxed wakefulness.

The modulation of 12.7 and 15.1 Hz was also assessed by the five planned comparisons. However, MEG in the dark bar condition was not significantly different from the equiluminant condition (see Table 1 for detail). Therefore, we conclude that the 10.2-Hz band is more definitely linked to MISC. This frequency corresponded very well with the perceived frequency of illusory jitter, though the correlation between peak alpha frequency and perceived jitter frequency across subjects was not significant.

Readers may notice that for the subject shown in Figure 3, activities around 1–5 Hz were reduced in the equiluminant condition. This tendency was not consistent across subjects, as can be seen in the group analysis (see Figure 4B). We also found that gamma band amplitudes

	2 vs. 1	2 vs. 3	2 vs. 4	2 vs. 5	2 vs. 6
10.3 Hz	0.03	0.003	0.02	< 0.001	0.002
12.7 Hz	0.47	0.007	0.01	0.01	0.03
15.1 Hz	0.24	0.02	0.005	< 0.001	0.08

Table 1. *P*-values of planned comparisons at around alpha frequency.

(40 Hz) tended to be smaller during illusory jitter (Figure 4B). This trend might indicate a failure to bind visual attributes in the critical equiluminant condition. However, this reduction did not reach statistically significant.

Discussion

In motion induced spatial conflict (MISC), a pattern that we know is moving rigidly and smoothly nevertheless appears to jitter at a characteristic frequency. We have shown here that MISC appears to be associated with enhanced brain oscillations around the same characteristic frequency.

We have also shown that these brain oscillations were enhanced during a condition that elicited robust illusory jitter (condition 2) relative to all other experimental conditions. This cannot be attributed to the spatial layout of the stimulus since illusory jitter (condition 2) and the concomitant alpha activity was markedly reduced by increasing luminance differences across stimulus boundaries (conditions 1 and 3) while keeping the spatial layout constant.

Our findings cannot be attributed to the simple presence of a near equiluminant moving border as alpha band activity was enhanced during illusory jitter relative to another two conditions with equiluminant borders but no illusory jitter (conditions 4 and 5). Perhaps most importantly, our findings cannot simply be attributed to jitter perception as alpha band activity was enhanced during illusory jitter relative to a final condition in which physical jitter (matched to the illusory jitter in terms of apparent frequency) was added to the stimulus (condition 6). The enhanced alpha band activity must therefore be a consequence of the *generation* of illusory jitter rather than a simple correlate of jitter perception.

We can also discount the possibility that our results are simply related to the small eye movements that are present even during target fixation. Such eye movements evoke little alpha band brain activity and they would have been present in all of our experimental conditions, in contrast to the illusory jitter and enhanced alpha band activity which was only evident during the equiluminant condition.

We believe that MISC arises as a consequence of a forward model whose function is to calibrate spatiotemporal vision. We propose that motion signals are used to compute a forward model of the spatial configuration. This model can then be compared against subsequent input. Such a system would be challenged by a moving stimulus containing both equiluminant and high luminance contrast borders, since the equiluminant (or chromatic) border is signaled as moving relatively slowly (Cavanagh, Tyler, & Favreau, 1984; Thompson, 1982). This could lead to a discrepancy between the predicted and current spatial pattern. We suggest that MISC is the visible consequence of the resolution of this conflict (Arnold & Johnston, 2003). The calibration process appears to be characterized by temporal sampling at a fixed rate, rather than by sampling based on the amount of conflict within the stimulus, as MISC rate does not appear to vary with stimulus speed (Arnold & Johnston, 2003). Our data here suggest that MISC is reflected in enhanced neural oscillations.

Both our psychophysical data and MEG recordings suggest a calibration sampling interval of ~100 ms. Van Rullen and colleagues (VanRullen & Koch, 2003; VanRullen, Reddy, & Koch, 2005) have also proposed a 100-ms sampling process in motion perception, after showing that reversals in the continuous wagon wheel illusion are maximal for windmill patterns rotating with a temporal frequency of ~10 Hz (VanRullen et al., 2005). They also showed that there is a reduction in the amplitude of EEG recordings within a narrow band around 13 Hz prior to the appearance of reversed motion (VanRullen, Reddy, & Koch, 2006). The proposal that there is a fixed rate of temporal sampling within the visual system is controversial (Holcombe, Clifford, Eagleman, & Pakarian, 2005; Kline, Holcombe, & Eagleman, 2004). Note, however, that here we are not arguing for temporal sampling of the motion sequence itself but rather for the temporal sampling of a forward model.

Conclusions

Modulation of coordinated neural activity has been considered to be integral to a number of cognitive and visual processes (Gho & Varela, 1988; Holcombe et al., 2005; Kline et al., 2004; VanRullen & Koch, 2003; VanRullen et al., 2005, 2006; Varela, Toro, John, & Schwartz, 1981). However, to date there has been no evidence that the particular frequency of the coordinated activity is tied to the temporal dynamics of perceptual experience.

Here we have reported an increase in the amplitude of alpha band neural oscillations when observing a stimulus that generates illusory spatial jitter. Both the frequency of the illusory perceptual experience and the frequency of the neural oscillations enhanced during the jitter perception were around 10 Hz. This offers the intriguing possibility that both arise from a common mechanism. We associate both phenomena with dynamic sampling within a calibration circuit, in which a motion-based forward model of a spatial pattern is compared against new input, thereby linking motion computation with spatial perception.

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