Stimulus Specificity of Phase-Locked and Non-Phase-Locked 40 Hz Visual Responses in Human

Catherine Tallon-Baudry, Olivier Bertrand, Claude Delpuech, and Jacques Pernier

Brain Signals and Processing Laboratory, Institut National de la Santé et de la Recherche Médicale, F-69424 Lyon Cedex 03, France

Considerable interest has been raised by non-phase-locked episodes of synchronization in the gamma-band (30–60 Hz). One of their putative roles in the visual modality is feature-binding. We tested the stimulus specificity of high-frequency oscillations in humans using three types of visual stimuli: two coherent stimuli (a Kanizsa and a real triangle) and a noncoherent stimulus (“no-triangle stimulus”). The task of the subject was to count the occurrences of a curved illusory triangle. A time–frequency analysis of single-trial EEG data recorded from eight human subjects was performed to characterize phase-locked as well as non-phase-locked high-frequency activities.

We found an early phase-locked 40 Hz component, maximal at electrodes Cz–C4, which does not vary with stimulation type. We describe a second 40 Hz component, appearing around 280 msec, that is not phase-locked to stimulus onset. This component is stronger in response to a coherent triangle, whether real or illusory: it could reflect, therefore, a mechanism of feature binding based on high-frequency synchronization. Because both the illusory and the real triangle are more target-like, it could also correspond to an oscillatory mechanism for testing the match between stimulus and target. At the same latencies, the low-frequency evoked response components phase-locked to stimulus onset behave differently, suggesting that low- and high-frequency activities have different functional roles.

Key words: vision; feature binding; synchronization; 40 Hz; oscillations; gamma-band; human; evoked potentials; EEG

M. liner (1974) presented a model for visual shape recognition in which synchronization of cell responses characterized a neuronal assembly coding for an object. This model suggested a mechanism for feature binding: cells responding to features belonging to the same object would discharge in synchrony. More recently, Singer’s and Eckhorn’s groups have reported experimental evidence for the existence of high-frequency synchronization in the visual cortex of the anesthetized cat, and checked the stimulus specificity of these oscillatory phenomena (Eckhorn et al., 1988; Gray and Singer, 1989; Gray et al., 1990; Engel et al., 1991). High-frequency (30–90 Hz) oscillations have also been described in the visual cortex of the awake macaque monkey (Reifer and Singer, 1992; Eckhorn et al., 1993; Fries et al., 1994). However, the role of high-frequency synchronization in feature binding remains controversial because other groups either did not find any oscillatory activity (Tovee and Rolls, 1992; Young et al., 1992) or had doubts about their putative functional roles (Ghose and Freeman, 1992).

In the visual modality, 30–40 Hz EEG activities in humans are known to be elicited either by periodic visual stimulation (so-called steady-state response) (Regan, 1968) or by a brief steady illumination (Chatrian, 1960). More recently, we reported the existence of a very small, although significant, increase of the averaged evoked potential around 32 Hz in response to coherent triangles, either real or illusory (Tallon et al., 1995). This component could be related to the oscillatory events observed in cat and monkey, because it seems dependent on stimulus coherency.
The signal was convoluted by complex Morlet's wavelets \( w(t, f_0) \) (Kronland-Martinet et al., 1987) having a Gaussian shape both in the time domain (SD \( \sigma_t \)) and in the frequency domain (SD \( \sigma_f \)) around its central frequency \( f_0 \): 
\[
 w(t, f_0) = A \cdot \exp(-t^2/2\sigma_t^2) \cdot \exp(2\pi i t f_0),
\]
with \( A = 1/2\pi \sigma_f \). Wavelets were normalized so that their total energy was 1, the normalization factor \( A \) being equal to \( (\sigma_t/\pi)^{-1/2} \). A wavelet family is characterized by a constant ratio \( f_0/\sigma_f \), which should be chosen in practice greater than \(-5\) (Grosman et al., 1989). The wavelet family we used was defined by \( f_0/\sigma_f = 1 \), with \( f_0 \) ranging from 20 to 100 Hz in 1 Hz steps. At 20 Hz, this leads to a wavelet duration \( 2\pi \) of 111.4 msec and to a spectral bandwidth \( 2\pi \sigma_f \) of 5.8 Hz and, at 100 Hz, to a duration of 2.2 msec and a bandwidth of 28.6 Hz. The time resolution of this method, therefore, increases with frequency, whereas the frequency resolution decreases. Below 20 Hz, wavelet duration is of hundreds of milliseconds for non-phase-locked and low-frequency components. Thus, long epochs of EEG data are required for proper analysis of gamma-band oscillatory activity, the time–frequency analysis of phase-locked and non-phase-locked components will be focused on the 20–100 Hz frequency range. Nevertheless, we will compare with a similar temporal resolution our results to the standard averaged evoked response (low-frequency phase-locked activity only).

The time–frequency energy \( E(t, f_0) \) of the signal in a frequency band around \( f_0 \) is the squared norm of the result of the convolution of a complex wavelet \( w(t, f_0) \) with the signal \( s(t) \):
\[
 E(t, f_0) = | w(t, f_0) \cdot s(t) |^2.
\]
A family of wavelets will provide a time–frequency representation of the energy of the signal (TF energy). This approach can be applied to the averaged evoked potential or each single trial. The TF energy of the averaged evoked potential allows us to characterize phase-locked activities, while averaging the TF energy of each single trial, both phase-locked and non-phase-locked activities are summed. In the latter case, noise energy is also added up: only high signal-to-noise-ratio activities will emerge. The mean TF energy of the prestimulus (between –200 and –50 msec) is considered as a baseline level and is subtracted from the pre- and poststimulus TF energy. This correction is done separately in each frequency band.

The phase-locking of the oscillatory burst can be evaluated in the time–frequency domain by adapting the “phase-averaging” methods previously proposed in the frequency domain by Jervis et al. (1983). We consider the normalized complex time–varying energy of each single trial \( E(t, f_0) = | w(t, f_0) \cdot s(t) |^2 \). Averaging these quantities across single trials leads to a complex value related to the phase distribution of each time–frequency region around \( f_0 \). The modulus of this value will be called the “phase-locking factor.” It ranges from 0 (purely non-phase-locked activity) to 1 (strictly phase-locked activity). With this method, very low-amplitude signals can be identified provided they are rather strictly phase-locked. Furthermore, it has been shown to be robust against artifacts. To detect phase ordering, a statistical test (Rayleigh test) of uniformity of angle is used (Jervis et al., 1983).

Because our data are far from having a normal distribution, the nonparametric Quade test for related samples and Conover procedures as post hoc tests of significance were used (Conover, 1980). This test is an extension of the Wilcoxon signed-ranks test to the case of several related samples. It is performed by ranking data paired by subjects and provides an \( F \) value indicating whether there is a statistically significant global effect of stimulation type. If the effect is significant, Conover procedures can determine in which pairs of experimental conditions significant differences occur. To reduce the effect of intersubject variability in frequency and latency, this test was applied to mean TF energy values within a 100 msec × 15 Hz window. This window was regularly shifted by 16 msec in time and 3 Hz in frequency to cover the entire time–frequency plane.

**RESULTS**

**Identification of three components in the time–frequency domain**

We first averaged the TF energy across single trials to analyze both phase-locked and non-phase-locked activities. Two successive components of the gamma-band (30–60 Hz) response can be seen at electrode Cz (Fig. 2, top row): one at ~90 msec, 40 Hz, and another one near 280 msec, extending from 30 Hz up to ~70 Hz. Between these two peaks, the level of 30–80 Hz energy is lower than in the prestimulus period.

![Figure 1.](image-url) Stimuli. We used three types of nontarget stimuli: an illusory triangle (Kanizsa triangle) (I), a real triangle (2), and what we called a “no-triangle stimulus” (3). Subjects were instructed to count silently the number of additional target distractor, a curved illusory triangle (4). This task, when correctly performed, ensured that subjects perceived illusory contours.

**Figure 1.** Stimuli. We used three types of nontarget stimuli: an illusory triangle (Kanizsa triangle) (I), a real triangle (2), and what we called a “no-triangle stimulus” (3). Subjects were instructed to count silently the occurrences of an additional target distractor, a curved illusory triangle (4). This task, when correctly performed, ensured that subjects perceived illusory contours.
Figure 2. Time-frequency analysis at electrode Cz, grand average across subjects. Top row, TF energy averaged across single trials. This type of averaging sums phase-locked as well as non-phase-locked activities. Results are baseline-corrected (subtraction of the prestimulus levels in each frequency band), thus producing positive and negative values. Two successive increases of TF energy can be observed: a first one around 90 msec and a second one around 280 msec. Middle row, Phase-locking factor. The first gamma-band component (90 msec) is phase-locked to stimulus onset, whereas the second one (280 msec) disappears; it is not phase-locked. Data are not baseline-corrected: the artifact created by our video monitor, therefore, is prominent (continuous component at 62 Hz, video frame rate). Bottom row, Baseline-corrected TF energy of the averaged evoked potential. Only phase-locked components of the response can be seen, but with a better signal-to-noise ratio. There are no TF energy differences between stimulation types for the 40 Hz, 90 msec component.

Both the 100 msec, 40 Hz and the 280 msec, 30–70 Hz components seem to be distinct from the lower frequency components of the response, because the TF energy decreases at ~25 Hz and increases again at higher frequencies. We will thus call “low frequencies” frequencies ranging from 0 to 25 Hz, and “high frequencies” those ranging from 25 to 100 Hz. Because the time-frequency analysis we developed gives a poor time resolution for frequencies below 15 Hz, low-frequency components will be studied in the 0–25 Hz filtered averaged evoked potential, whereas time-frequency representations will be used for high-frequency components.

The second step in our analysis was “phase averaging”: it allows characterization of phase-locked activities regardless of their amplitude. Results at electrode Cz are shown in Figure 2 (middle row).

Both the 100 msec, 40 Hz and the 280 msec, 30–70 Hz components seem to be distinct from the lower frequency components of the response, because the TF energy decreases at ~25 Hz and increases again at higher frequencies. We will thus call “low frequencies” frequencies ranging from 0 to 25 Hz, and “high frequencies” those ranging from 25 to 100 Hz. Because the time-frequency analysis we developed gives a poor time resolution for frequencies below 15 Hz, low-frequency components will be studied in the 0–25 Hz filtered averaged evoked potential, whereas time-frequency representations will be used for high-frequency components.

The second step in our analysis was “phase averaging”: it allows characterization of phase-locked activities regardless of their amplitude. Results at electrode Cz are shown in Figure 2 (middle row).

The 90 msec, 40 Hz component appears to be phase-locked to stimulus onset. Indeed, all subjects show a significantly phase-locked component around 90 msec and 40 Hz (Rayleigh test at electrode Cz: p < 0.001 for 7 of 8 subjects, p < 0.01 for all subjects). This part of the response will be studied, therefore, in the time–frequency representation of the energy of the averaged evoked potential, to be in a better signal-to-noise ratio situation (Fig. 2, bottom row). The second gamma-range component disappears completely on the time–frequency representation of the phase-locking factor. This component, therefore, is not strictly phase-locked to stimulus onset and will be studied on the TF energy averaged across single trials.

A continuous phase-locked activity centered at 62 Hz appearing on the time–frequency representation of the phase-locking factor corresponds to the frame rate of the video monitor on which stimuli were delivered. This activity is continuous (same level on the pre- and poststimulus TF representation of the phase-locking factor), and thus disappears on baseline-subtracted representations of TF energy (Fig. 2, top and bottom rows).

We thus found two different types of high-frequency activities: an early one (90 msec) phase-locked to stimulus onset, and another one appearing later (280 msec), not phase-locked to stimulus onset. Both responses seem to be distinct from low-frequency potentials (0–25 Hz). These results are similar at all electrodes.

These findings led us to divide the entire electrical response into three components, each one analyzed using the appropriate method:

1. **Low-frequency phase-locked components (0–25 Hz):** analysis of the low-pass-filtered averaged evoked potential.
2. **Phase-locked, high-frequency early components (20–100 Hz, 0–200 msec):** analysis of the TF energy of the averaged evoked potential.
3. **Non-phase-locked, high-frequency late components (20–100 Hz, 200–500 msec):** analysis of the TF energy averaged across single trials.

### First burst (TF energy of the averaged evoked potential)

The first burst of 40 Hz activity is phase-locked to the stimulus onset and thus appears with a better signal-to-noise ratio on the time–frequency representation of the energy of the averaged evoked potential (Fig. 2, bottom row).

This first 40 Hz component shows a clear maximum at electrodes Cz and C4, as depicted in Figure 3. There does not seem to be any difference between experimental conditions at these electrodes. To confirm this, we first searched for the maximal TF energy across electrodes, for each subject and each stimulus condition. This maximum always occurred at electrode Cz or C4, except for one subject whose maximum appeared at P4. We

---

**Table 1. Energy, latency, and frequency of the maximum of the first 40 Hz response, measured on the TF energy of the averaged evoked potential**

<table>
<thead>
<tr>
<th>Energy (μV²)</th>
<th>Latency (msec)</th>
<th>Frequency (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Illusory</td>
<td>Real</td>
<td>No</td>
</tr>
<tr>
<td>Mean</td>
<td>19.5</td>
<td>21.9</td>
</tr>
<tr>
<td>SEM</td>
<td>5.4</td>
<td>4.8</td>
</tr>
</tbody>
</table>

No significant differences can be found among conditions.
measured its TF energy, latency, and frequency. Results are summarized in Table 1: the maximal TF energy does not vary with stimulation type. It tends to appear later in the illusory triangle condition, and at a higher frequency in the real triangle condition, but neither of these two observations is significant (Wilcoxon test for matched pairs, \( p > 0.1 \)).

We then performed a Quade test on the time-frequency representation of the energy of the averaged evoked potential, at electrodes Cz and C4, in smoothing windows of 100 msec × 15 Hz, shifted by steps of 16 msec in time and of 3 Hz in frequency (between 0 and 200 msec, and between 20 and 100 Hz). This analysis confirmed that there were no significant differences between stimulation types.

Second burst (TF energy averaged across single trials)

The topography of the second burst is less clear than the topography of the first burst: on data averaged across subjects (Fig. 4), no clear maximum can be found, even though the TF energy at posterior electrodes seems slightly higher than at anterior ones. We searched for the location of the maximal TF energy between 250 and 350 msec, and between 30 and 70 Hz, for each subject and in each condition. In seven of eight subjects, this maximum is reached at electrodes posterior to Pz in all experimental conditions.

Visual inspection of filtered single trials on which a 30-45 Hz component could be identified confirms this widespread topography, as well as the posterior location of the maximum (Fig. 5). No polarity inversion can be observed. Furthermore, it appears that (1) the oscillatory events are rather short (from 100 to 150 msec),
(2) their amplitude can reach up to 10 μV, and (3) the latency of the maximal positive peak can vary by at least as much as 37 msec.

The intersubject variability of this second burst is quite strong, in energy as well as in frequency, as depicted in Figure 6.

TF energy variations with stimulation type seem distributed over all of the electrodes, with a high response to the illusory triangle, an intermediate response to the real triangle, and a weak (or even sometimes below baseline) response to the no-triangle stimulus (Fig. 4).

We performed a Quade test on the time–frequency representation of the energy averaged across single trials, at each electrode, in smoothing windows of 100 msec × 15 Hz, shifted by steps of 16 msec in time and of 3 Hz in frequency (between 200 and 500 msec and 20 and 100 Hz). At all electrodes but Iz, O2, T6, and Fz, the test shows a significant effect of the stimulation type in a window centered at 250 msec and 35 Hz. The size of this window (mainly its time–length) varies with electrodes (Fig. 7). The effect is confined to the 30–40 Hz range: no effect can be found at higher frequencies.

Within this region (around 250 msec and 35 Hz) where a significant stimulus effect is found, the Conover procedures show two types of effects: either the response to the illusory triangle is significantly

Figure 6. TF energy averaged across single trials of four different subjects, at electrode POz, in response to the illusory triangle. Note the strong intersubject variability of the non-phase-locked, 280 msec component (energy of the maximum ranging from 40 to 150 μV² and frequency from 25 to 65 Hz).

Figure 7. Quade test: F-values at electrodes POz and Cz. A Quade test was performed on the energy averaged across single trials, on 100 msec × 15 Hz moving time–frequency windows. F > 3.74 (in white) at (x, y) msec and Hz indicates a significant effect (p < 0.05) of the stimulation type in the 100 msec × 15 Hz time–frequency window centered in (x, y). The duration of the significant effect may vary from electrode to electrode, but the effect is always confined to the 30–40 Hz range.

stronger than the response to the no-triangle stimulus, or both the responses to the illusory and the real triangles are significantly higher than the response to the no-triangle stimulus (Quade test and Conover procedures, p < 0.05). The energies of the real and of the illusory triangles are never significantly different.

At each electrode at which an effect of the stimulation type could be found, we searched for the largest time-frequency window in which both the responses to the illusory and the real triangle were significantly higher than the response to the no-triangle stimulus, and for the largest time-frequency window in which the response to the illusory triangle was significantly higher than the response to the no-triangle stimulus. Results are shown on Table 2. It appears that in a 200–300 msec, 30–40 Hz window, both the real and the illusory triangles give rise to a stronger response than the no-triangle stimulus, and that between 300 and 400 msec, and 30 and 40 Hz, only the difference between the illusory and the no-triangle stimulus remains significant. Within this region, the TF energy of the response to the real triangle is intermediate between the two others.

Low-frequency averaged evoked potentials (filtered 0–25 Hz)

The usual complex of a first positive peak (P1) followed by a negative one (N1) can be observed in the averaged evoked potentials in response to the three stimuli. These two components are maximal at occipital electrodes (P1: O1, O2, or POz; N1: T5, O1, O2, or T6, depending on the subjects). We measured the P1 and N1 maximal amplitude values and their peak latencies, for each subject in each condition (Table 3). No differences among stimulus types could be found.

Later on, two successive effects can be found in the evoked potentials, as depicted in Figure 8 (Quade test and Conover procedures applied on 100 msec time windows regularly shifted by 20 msec, p < 0.05). The first appears between 200 and 300 msec and corresponds to a more negative potential in response to the illusory triangle than to the two other stimuli. This effect can be found at all electrodes, but appears earlier at occipital electrodes. The second effect appears between 300 and 400 msec, and corresponds to higher values of potential for the real triangle than the two others. It affects a more limited set of electrodes, on the right side of the head (Fig. 8). Both effects are mainly attributable to the very low-frequency components of the evoked potential (<8 Hz); they are no longer significant in the 8–25 Hz filtered evoked potentials.

**DISCUSSION**

We thus found the following:

- around 90 msec a 40 Hz component, phase-locked to the stimulus onset, appears. This component is maximal at electrodes Cz and C4. At the same time, the first positive peak (P1) of the low-frequency evoked potential is rising. It reaches its maximum at 113 msec at occipital electrodes (O1, O2 or POz, depending on the subjects). The different topographies of the low- and high-frequency phase-locked components are shown in Figure 9. Neither these two components vary with stimulus type.
  - between 200 and 300 msec, a non-phase-locked, 30–40 Hz component appears. It is significantly stronger in response to both real and illusory triangles. At the same time, a very low-frequency component (0–8 Hz) appears in the evoked response. This component is more negative in response to the illusory triangle than to the real or the no triangle. Both these low- and high-frequency effects are rather spread out on the scalp and are significant at most electrodes.
  - between 300 and 400 msec, the non-phase-locked, 30–40 Hz component is significantly stronger in response to the illusory triangle than in response to the no-triangle. The 40 Hz response to the real triangle is intermediate between the two others. At the same latencies, low-frequency evoked potentials are more positive in response to the real triangle compared with the illusory or the no-triangle stimulus.

The functional role of the first 40 Hz, phase-locked component remains unclear. An early 40 Hz component appearing in averaged evoked potentials has been described by Jokeit et al. (1994) in response to a visual stimulus in a priming reaction time task. It may be that this component appears in response to any visual stimulus in any task. This 40 Hz component could also be part of a broad-band activity including the P1 low-frequency component, because neither of these two components varies with stimulation type. Still, their topographies and latencies are different, suggesting that they reflect the activity of different neural sources.

In the auditory modality, an early, transient 40 Hz response can be observed in the averaged evoked potential (Galambs et al., 1981; Pantev et al., 1991) and has been suggested to reflect the activation of thalamo-cortical loops (Ribary et al., 1991; Llinàs and Ribary, 1993). Both the early 40 Hz response and the low-frequency potentials have similar topographies (Bertrand and Pantev, 1994), whereas in the visual modality, they are quite different. We do not know yet whether there is a functional analogy between the two modalities.

Short-latency, stimulus-locked, high-frequency responses in V1 of the behaving macaque monkey have been described (Mansell and Gibson, 1992). There is quite a difference in the latency of the two phenomenon (before 50 msec in monkey, and around 90 msec in human) and in their frequency (50–100 Hz in monkey, 40 Hz in human). Furthermore, an activity restricted to area V1 is not likely to appear on the scalp with a maximum at electrodes Cz and C4. It is still possible that the phase-locked activity we observe on the scalp reflects a combination of activation in V1 and other areas.

The non-phase-locked 40 Hz component occurring between 200 and 400 msec varies with stimulation type: it is stronger in re-
response to a coherent triangle, whether real or illusory. At least two mechanisms can account for this: (1) an oscillatory mechanism of feature binding as suggested by Singer’s and Eckhorn’s groups (Engel et al., 1992; Eckhorn, 1994): neurons responding to the triangle (real or illusory) would discharge in synchrony around 35 Hz, or (2) an oscillatory matching mechanism between an internal representation of the target stimulus (curved triangle) and the occurring stimulus. Because both the illusory and the real triangles look more like the attended target, they may give rise to a stronger matching. A possible control would be a target stimulus looking more like the no-triangle stimulus. Nevertheless, the correct perception of illusory contours would not be ensured in such an experimental design. This raises the problem of the links among the processes of perception, recognition, and attention. Many different stimulus types and tasks will have to be used to determine whether the non-phase-locked 40 Hz component we observe in humans does reflect feature binding, visual matching, or another mechanism of perception.

It seems unlikely that this component could correspond to muscle activity, because the effect is confined between 30 and 40 Hz. If muscle activity were involved, one would expect to find at least some effects at higher frequencies (>60 Hz), and the topography of the activity would probably not show a maximum at parieto-occipital electrodes. It also seems unlikely that this com-

---

**Figure 8.** 
**A.** 0–25 Hz filtered averaged evoked potentials. We performed a Quade test and Conover procedures on the averaged evoked potential, computed over 100 msec time windows regularly shifted by 20 msec. Two successive effects can be found. They are plotted on the figure as dots or bars indicating the center of the 100 msec time window on which an effect has been found. A first effect occurs on all of the electrodes between 200 and 300 msec; it corresponds to potentials more negative for the illusory triangle than for the two others (dots). The second effect concerns a more limited set of electrodes and appears between 300 and 400 msec. It corresponds to a greater positivity in response to the real triangle than the two others (bars). **B.** Topography of the 0–25 Hz averaged evoked potential (grand average across subjects) at two latencies (250 and 380 msec) in each condition. At 250 msec, the response to the illusory triangle shows a more pronounced negativity at occipital and parietal electrodes. At 380 msec, the real triangle elicits a more positive response than the two others on the right side of the scalp.
with the 30–50 Hz filtered evoked potential (thick lines) of the evoked response. The broad-band averaged evoked potential for the contour, whether real or perceptually generated, "located which (1) suggests the existence of a "common locus of processing "occur in multiple foci."

Because the origin of the scalp-recorded activity we observe is not known, it is difficult to compare it directly with local field potentials or multi-unit activities recorded from a few neurons within one or two areas in the animal. Nevertheless, the 40 Hz activity we observe shows some similarities with the oscillatory events elicited by a visual stimulus recorded in the animal:

- the scalp-recorded activity is not phase-locked to the stimulus onset, like the oscillatory events recorded in cat (Eckhorn et al., 1988; Gray and Singer, 1989; Gray et al., 1989, 1990, 1992; Brosch et al., 1995) and in monkey (Eckhorn et al., 1993).
- the activity we describe lasts between ~100 and ~150 msec. Oscillations in local field potentials have been estimated to last from 100 to 200 msec in the anesthetized cat (Gray et al., 1992), and from 100 to 300 msec in the superior temporal sulcus of the awake monkey (Kreiter and Singer, 1992). Irregular bursts in the 20–40 Hz of the monkey EEG last between 75 and 200 msec (Freeman and van Dijk, 1987).
- both the activity we describe and the high-frequency synchronization observed by Gray et al. (1989) and Engel et al. (1991) are stronger in response to coherent stimuli.

All of these comparisons are made with experiments on animal using moving stimuli, whereas those we used in our study were stationary. Stationary stimuli have been shown to elicit few or no oscillatory events in cat (Gray et al., 1990) and monkey (Tovee and Rolls, 1992; Young et al., 1992). Nevertheless, Gray et al. (1995) reported recently that stationary stimuli actually elicit oscillatory events in the awake monkey.

Low-frequency evoked potential components display an increased negativity in response to the illusory triangle between 200 and 300 msec, as already found by Sugawara and Morotomi (1991). The effect we observe in low-frequency potentials is distinct from the effect found in the 40 Hz range, indicating that high- and low-frequency components of the response have different functional roles. Still, the precise role of this low-frequency component (0–8 Hz) remains unclear, as well as its origin. Neurons in V2 (von der Heydt et al., 1984) as well as in V1 (Grosos et al., 1993) have been shown to respond to illusory contours, but we have no evidence yet that the low-frequency negativity associated with processing of illusory contours we observe originates in V1/V2.

Probably both low- and high-frequency synchronizations participate in the processing of the illusory and real triangles, but in different manners. The functional links between these two types of activities remain to be explored, and functional models integrating low- and high-frequency activities devised.

REFERENCES


