Abstract

This informal report summarizes my findings in the literature regarding the hypothetical modulation of human brain oscillations by motor vehicle vibrations. Hypothetically, vibrotactile stimuli delivered to motor vehicle passengers may modulate their oscillatory neural activity, inflicting on cognitive performance and vigilance level.

Methodology – First, the analogous phenomena in the auditory and visual modalities are reviewed. The somatosensory response to tactile and vibrotactile stimuli is then reviewed in better detail. The vibrational spectra in motor vehicles are qualified, along with the vibrational power absorption curves of adult and infant passengers. We then review the existing experimental evidence for the neural and cognitive effects of vertical whole-body vibrations, in adult and infant humans. Finally, some candidate neural rhythms for modulation by motor vehicle vibrations are suggested.

Findings & Conclusions – Cerebral neural oscillations in the alpha band (7-14 Hz for adults, 4-11 Hz for infants) are a leading candidate for modulation by motor vehicle vibrations. Their functional role is reinterpreted as associated with maintenance of alertness, to comply with their diverging experimental manifestations. For 1-2 years old infants, the peak frequency of alpha-band neural oscillations matches the frequency of peak power absorption of vertical whole-body vibrations. Accordingly we suggest, that infants at this age group should be more susceptible to entrainment of their neural alpha activity by whole-body vibrations. The fact that rocking stimuli soothes 0-6 months old infants argues against the involvement of the later-appearing alpha oscillations in the neural process underlying this soothing effect. Instead, we speculate that the prominent ~13 Hz component of motor vehicle vibrations may lead to improved synchronization of 7-15 Hz spindle oscillations, thereby promoting sleep in infant and adult humans alike.

Suggestively, some novel findings are identified in earlier studies, which were not reported by their authors. This especially holds for the non-linear components of the neural response to rhythmical vibrotactile stimuli. These suggested findings provide new insights to the hypothesis investigated in this report, but are not essential for its validation.

Existing experimental evidence is apparently too sparse to confirm or refute the hypothetical modulation of neural oscillations by temporally patterned sensations, induced by motor vehicle vibrations. Specifically, we don't know if this hypothetical modulation has anything to do with the underlying processes by which rocking elicits sleep in infants. Present-day technology enables performing insightful neuroscientific research, which will hopefully shed light on these fascinating phenomena.
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1. **Introduction**

This informal report summarizes my findings in the literature regarding the hypothetical modulation of human brain oscillations by motor vehicle vibrations.

1.1. **Motivation** – In Oscar Wilde's novel 'The Picture of Dorian Gray', Dorian wonders [200]:

> "If thought could exercise an influence upon a living organism, might not thought exercise an influence upon dead inorganic things? Nay, without thought or conscious desire, might not things external to ourselves vibrate in unison with our moods and passions, atom calling to atom in secret love or strange affinity?"

Here we pose a more moderate question – could vibrations external to ourselves affect our cognitive state? The plain answer is positive – severe vibrations elicit discomfort or pain, whereas massaging vibrators elicit relaxation. Yet on the neuroscientific level, a surprisingly low number of studies have investigated how a given vibratory stimulus may modulate the neural electromagnetic activity in the human brain. Apparently none of these studies searched for a cognitive effect accompanying such a modulation. As previous studies reported a clear cognitive effect for certain kinds of rhythmical auditory and visual stimuli, it is interesting to look for their somatosensory analogue.

It is especially intriguing to investigate the possible cognitive effects of vibrations experienced by passengers in motor vehicles. A human passenger traveling in a common family car is continuously exposed to mechanical vibrations, mostly in the 1-100 Hz frequency range. Human somatosensory perception entirely covers this frequency range, which also matches the frequency bands of the major neural oscillations, during wakefulness and sleep. Could the human spectrum of sensations and feelings be influenced by motor vehicle vibrations? It is tempting to relate this hypothetical influence to the ease in which infants fall asleep in traveling cars.

1.2. **Partial Terminology of Neural Oscillatory Responses** – Some recurrent terms used throughout this survey could use a brief introduction. In EEG & MEG studies, an amplitude enhancement in a given frequency band is called 'synchronization', whereas a decrease in amplitude is called 'desynchronization' [29,65]. A change in frequency band power may be both time-locked and phase-locked to a given stimulus or event, in which case it is called an 'evoked' response. Alternatively, if this change is time-locked to the stimulus, but jitters in phase between trials, it is called an 'induced' response. The induced activity is usually not revealed by traditional averaging techniques [65]. Furthermore, fMRI and PET measurements are sensitive to increases in overall neural activity, and not to changes arising from phase-locking alone, that may be reflected in EEG\MEG recordings [83]. At present, the extent to which stimulus locking and amplitude changes reflect distinct processes remains unclear [58,75,83,84].

Pre-stimulus activity is sometimes called 'spontaneous' activity, whereas post-stimulus activity that is not time-locked to the stimulus is referred to as 'ongoing' or 'undriven' activity [76]. Ongoing activity was traditionally treated as background noise masking the evoked response components. This approach is still of clinical use but its neuroscientific validity has been eventually controverted [29,75], as discussed hereunder in section 5.
1.3. **Road Map** – Before plunging into details, I’d like to sketch out the directions I took in approaching this problem. This would help pointing out the dead ends I stumbled at, as well as possible routes I haven’t noticed. The following block diagram illustrates the structure of this report:

Dashed blocks represent an initial speculation, later abandoned due to the much higher neural coherence observed during sleep than during wakefulness. The developmental block was added once I realized that the differences between the EEG/MEG spectra of adults and infants may inflect on the hypothetical modulation of their brain activity by motor vehicle vibrations.
2. Auditory Modulation of Neural Oscillations

Auditory steady-state response (ASSR\textsuperscript{1}) is a remarkable neurophysiological phenomenon. Rhythmical auditory stimuli at various frequencies elicit a time locked steady-state response, which peaks in amplitude for a stimulation frequency of about 40 Hz, with smaller amplitudes at lower and higher stimulation frequencies [3]. ASSRs can be elicited by a variety of periodic stimuli such as clicks, pure tones, and amplitude or frequency modulation of continuous sounds [32]. They are astonishingly well time-locked to the eliciting stimulus [2].

Fortunately there's an ample literature on this subject, since its identification by Galambos et al. in 1981 [1] to these days. I shall only cite some of the relevant findings reported in several important studies.

2.1. Uniqueness of 40 Hz ASSR – The cause of maximal response at stimulation rates around 40 Hz has been intensely debated. Galambos et al. [1] originally suggested that the 40 Hz peak merely corresponds to a superposition of middle latency auditory evoked potentials. Alternatively, it could reflect a true increase in cortical synaptic activity, a resonance phenomenon indicating the preferential working frequency of the auditory network [3,50,52]. Pastor et al. [3] used EEG and PET to investigate this issue. The stimuli were clicks applied monaurally to the right ear at 12 frequencies in the 12-60 Hz range. The authors hypothesized that the enhanced response at 40 Hz reflects increased synaptic cortical activity, and that brain regions outside the auditory cortex are activated specifically by stimulation at 40 Hz and not at other gamma frequencies. Their reported grand-averaged frequency response is a clear exemplar of the ASSR phenomenon. Pasted to its right is the grand-averaged amplitude at the frequency of the auditory stimulus:

![Grand-averaged spectrograms of ASSR at electrode site F3 (left) and grand-averaged amplitude at stimulus frequency (right). Adapted from [3].](image)

Three major components can be identified in this plot. First, a 10 Hz component with an occipital predominance, corresponding to neural activity in the alpha frequency band. A second component is the evoked response at the frequency of the auditory stimulus. Its amplitude varies with frequency, peaking at ~40 Hz. Finally, a peak at 40 Hz is observed when the stimulus frequency 10 or 20 Hz, i.e. subharmonics of 40 Hz.

\textsuperscript{1}Also called SSR [32,51,52,135,136] or Amplitude Modulation Following Response (AMFR) [37,50,56].
The PET study revealed that all the probed stimulation frequencies (12, 32, 40 and 47 Hz) increased the regional cerebral blood flow (rCBF) at the temporal cortex, but only the 40 Hz increased rCBF at the cerebellar clusters.

To explain this finding, the authors postulated that the cerebellum becomes more active to inhibit excessive cortical firing elicited by the 40 Hz stimulation. As cortical excitability is reduced when the cerebellar cortex is electrically stimulated, the cerebellum suggestively has a cortical inhibitory role.

In the context of this survey, this study finds evidence for activation of other brain regions, outside the auditory cortex, only for the 40 Hz stimulation. However, as only three other frequencies were probed using PET – 12, 32 and 47 Hz – modulation of ongoing brain activity was not ruled out for other stimulation frequencies.

ASSR originates from multiple generators, localized to sites in the auditory pathways of the brain stem, as well as the primary and secondary auditory cortices [56,132-4,137]. Notably, cortical sites are more involved in the generation of ASSRs at frequencies below ~50 Hz [56,132]. Thus 40 Hz ASSR reflects the activity of higher neuronal ensembles, which are possibly not fully developed in neonates (see section 10.2).

2.2. **ASSR at Higher & Lower Gamma Frequencies** – Artieda et al. [50] applied a novel chirp-modulated tone stimulation to quickly probe ASSR at multiple frequencies. The stimulus consisted of a 1200 Hz tone modulated in amplitude by a linear chirp, i.e. a sinusoid whose frequency increased linearly from 1 to 120 Hz within 1.6 seconds. EEG analysis clearly revealed a diagonal band of energy, corresponding to the instantaneous frequency of the stimuli. This band clearly reflected an oscillatory response which was phase-locked to the stimuli. The authors reported that “this response began approximately at a stimulation frequency of 20 Hz and lasted till the end of the stimulus (120 Hz)”.

However, only the frequency range of 20 Hz and up is shown in this paper:
Two components were present in the diagonal band, a major one around 45 Hz (30-60 Hz) and a minor one in the 80-120 Hz range. Also clearly present in the following phase-locking diagram (fig. 4) were weaker diagonals, phase-locked to the first and second harmonics of the stimulus frequency, most clearly at the harmonics’ ~40 and ~80 Hz components:

Phase-locking to the first harmonic is highly statistically significant as it is visible in a phase-locking diagram averaged over 480 sweeps (fig. 4 right). However it is not reported by the authors. I have no idea why the authors chose not to present the neural frequency response below 20 Hz, and not to report the phase-locking at harmonics of the stimulus frequency. This is especially intriguing as a similar study in the visual modality [74] (see section 3.1) has found both a strong response in the alpha band to multiple stimulation frequencies, and significant responses at several harmonics of the
stimulation frequency. As a typical 8-10 Hz alpha activity is localized close to the auditory cortices, also known as the 'tau rhythm' [64,65,125], its possible modulation by rhythmical stimuli is naturally of high interest.

An earlier study by Ross et al. [135] has also reported clear phase-locking to the first and second harmonics of a given AM stimulus, peaking at ~22 and 40 Hz:

The given curve was obtained by normalizing the ASSRs of eight subjects according to their amplitude at 40 Hz. In two of the eight subjects, ~20 Hz ASSR was higher than 40 Hz ASSR. The 40 Hz peak was conserved in frequency along all eight subjects, whereas the ~20 Hz peak exhibited inter-individual variations of up to ~10 Hz.

2.3. ASSR at Lower Frequency Ranges – The auditory sensory system is well known for its ability to demodulate a given auditory input, extracting the information carried by its low-frequency envelope. Neural processing is adapted for the encoding of naturally occurring modulation information, such as phonemes (~4-30 Hz), syllables (~3-9 Hz) and words (~1-4 Hz) [130]. Signal demodulation begins at the cochlear level, with both low and high frequency components transmitted by auditory nerve fibers, who have the striking capability to phase-lock to signals up to several Kilo-Hertz [130,133]. Thalamic neurons are also capable of AM phase-locking over a wide range from a few Hertz to several hundred Hertz, allowing further spectral manipulations of the auditory input [130].

The 1-20 Hz frequency range has been less frequently probed in ASSR studies, possibly because pure tones cannot be used due to the diminished auditory sensitivity in this range. As part of the abovementioned study by Ross et al. [135], The 10-20 Hz frequency range has been probed in 2 Hz steps. As we saw in figure 5 above, the ASSR at the fundamental stimulus frequency is always stronger than that at any of its harmonics. Nevertheless, due to the ~1/f distribution of ongoing neural activity, the first harmonic of the response to 10-14 Hz stimuli (20-28 Hz respectively) was more distinguished from ongoing activity than that at the fundamental stimulus frequency. Consequently, when the ongoing activity is filtered out, the first harmonic of the driven response seems to be higher than that at the stimulus frequency, as evident figure 6 (left):
A similar trend has been observed for a 2 Hz stimulus, obtained by modulating a 250 Hz carrier by both 38 and 40 Hz modulators [136], as evident in figure 6 (right).

The observed spectrogram demonstrates the high nonlinearity of the auditory response. As denoted by the authors in [136]: “If the combination of the 38 and 40 Hz signal were processed by a second order nonlinear system, distortion products below 100 Hz would occur at 2, 76, 78 and 80 Hz, whereas the third order distortion products would contribute with spectral peaks at 36, 38, 40 and 42 Hz.” Instead, six 2-12 Hz peaks are significantly observed, accompanied by dominant peaks at 38 and 40 Hz and minor peaks at 42 and ~80 Hz. We shall later see interesting evidence for such highly nonlinear low frequency response, both in the visual and somatosensory modalities.

Interestingly, a single study [131] reported marked inter-hemispheric differences in the response to low frequency AM stimuli. The right posterior part of the superior temporal gyrus and the primary auditory cortex exhibited larger response to 8 Hz than to 4 Hz stimuli, whereas the left homologous areas were equally sensitive to either stimulus. As this frequency range is crucial for speech intelligibility, this finding may suggest interhemispheric differences in the processing of slow temporal modulations.

2.4. Cognitive Performance Reflects ASSR – Burle & Bonnet's study [41] provides a convincing linkage, between the mean scanning time at the Sternberg task, and the frequency of concurrent auditory clicks. In this experiment, six adults performed the Sternberg task while listening to auditory clicks at six frequencies in the 19.5-22 Hz range. For all six subjects, the reaction time (RT) decreased as stimulation frequency increased. The mean slope of the RT decrease was -2.3 ms/Hz, a mild but statistically significant effect (p<?). The authors suggested that ~40 Hz gamma oscillations were entrained by the ~20 Hz auditory stimuli. Suggestively, this so-called “speeding up of the internal clock” lead to the observed decrease in reaction time.
A cerebellar suppressive response to a 40 Hz stimulus alone, as reported in [3] (see above), might explain why Burle & Bonnet found the ~20 Hz stimuli more useful than a ~40 Hz stimuli. Moreover, if one assumes that the neural activity outside the auditory cortex cannot be entrained by the rhythmical stimuli, these findings may be explained by mental recitation of the visually presented items, a mental task involving the auditory cortex. Nevertheless, as we will later see in the visual modality (see section 3.6), what looks like the entrainment of 40 Hz oscillations reflected in cognitive performance [78], may seem to be a more puzzling neural response in EEG \ MEG recordings [79]. Specifically, the ~20 Hz stimuli might have modulated the auditory ~10 Hz tau rhythm [64,65,125]. The tau rhythm is known to be modulated during cognitive tasks, such as the recall of visual semantic memory [125], thus it might also play a role in performing the Sternberg task. We will later see further evidence for such subharmonic modulation of alpha activity by higher stimulus frequencies, in the visual modality and possibly in the tactile modality as well. Therefore, this study [41] convincingly demonstrated that rhythmical auditory stimuli may affect cognitive performance, but further measurements using neuroimaging tools are required to qualify this phenomenon.

2.5. **Attentional Effects on ASSR to Binaural Beats** – Two simultaneous pure tones of adjacent frequencies may be heard as one tone, with a pitch at their mean frequency, beating at a rate equal to the difference between both frequencies [130,133]. This kind of stimulus is called an 'acoustic beat'. A beating tone may also be heard when each sinusoidal component is presented, in isolation, to a different ear. This 'binaural beat' is a much fainter sensation, restricted to frequencies of up to a few hundred Hertz. The combination of cochlear inputs from both ears is assumed to first occur in the medial superior olive nucleus [133]. A frequency difference of less than 2 Hz is perceived as a sound moving from side to side, whereas higher frequency differences are perceived as loudness fluctuations, eventually inducing a sensation of a rough sound [130,133].

Schwarz & Taylor [133] demonstrated that a 40 Hz binaural beat elicited a clear 40 Hz ASSR in eighteen subjects. Both acoustic and binaural beats were generated, with a mean frequency of either 400 Hz (i.e. 380 and 420 Hz) or 3.2 kHz (i.e. 3.18 and 3.22 kHz). Maximal monaural or binaural beat ASSR amplitudes were recorded over the fronto-central region, usually at Cz and Fz electrode sites. The acoustic beats elicited clear 40 Hz ASSRs, both with the 400 and the 3200 Hz carrier. The binaural beat only elicited a 40 Hz ASSR with the 400 Hz carrier, suggesting degraded phase-locking at 3.2 kHz.

Importantly, attending to the two disharmonious input tones, rather than to one beating combination tone, eliminated all signs for a binaural beat ASSR. No such effect was observed when acoustic beats were used. This finding was incidentally discovered when a few subjects attempted to assign a musical interval to the two tones in different ears. This attentional effect will be likely elucidated by future studies.

2.6. **Supporting Pseudo-Scientific Testimonies** – Several commercial firms sell pseudo-scientific auditory products whose usage allegedly “results in brain wave entrainment and can induce altered states of consciousness”\(^2\). If their products are indeed more effective than placebo, regardless of their credibility, it may support the hypothesis that entrainment of whole brain activity by auditory stimuli is not limited to the modulation of 40 Hz gamma activity. However, the testimonies brought in these companies' websites describe various dramatic effects on cognition, whereas all the scientific literature I have found does not report any dramatic effect by any kind of mild sensual stimuli (except prolonged sensual deprivation). The only possibly dramatic effect that is widely reported,

\(^2\) Cited from the website of Intelegen Inc. ([http://web-us.com/](http://web-us.com/))
studied [85] and replicated is a certain kind of visual hallucinations, evoked by rhythmical visual stimuli at around 10-15 Hz (see following section 3.4).

2.7. Desynchronization of ASSR – Ross et al. [2] used MEG recordings to investigate the desynchronization of a 40 Hz ASSR by a short noise burst. When delivered alone, the monaural AM stimulus elicited a 40 Hz ASSR continuing for the duration of the AM sound, whereas the short noise burst evoked almost two cycles of gamma band oscillations. The responses were mainly of opposite polarity, thus a summation of them would have been reflected in an amplitude decrement of the ASSR. However, the perturbing stimulus induced a clear decrement of the total oscillatory activity, lasting much longer than the effect simulated by superimposition of responses. The ASSR decrement was smaller when the noise pulse was presented at the AM maximum. Amplitude enhancement was not observed under any stimulus conditions.

The time courses of ASSR amplitude and phase during recovery from the perturbation resembled those obtained after the stimulus onset. The change in the time course of the ASSR induced by the perturbation was thus interpreted as a new stimulus onset following a reset of activity. Moreover, the perturbing stimulus consistently induced a decrease of 3-5 ms in ASSR latency, corresponding to a phase shift of ~60-90° at 40 Hz (see figure 7). This phase shift, reported in several earlier studies (see also [78-9]), is interpreted by the authors as a reset of oscillations which shifts the ASSR phase back to the phase of the driving source. As the article is well written, I’d rather cite some of its other findings in their words: “Our results provide strong support for classifying the ASSR as a type of stimulus-driven oscillatory brain activity, rather than an evoked response. [...] The ASSR is more likely induced activity, which is facilitated by the rhythmic stimulation with frequencies close to the best responding frequency of the underlying neural network. [...] The finding of a power increase, during the 40-Hz stimulation, suggests that the ASSR is generated in addition to ongoing spontaneous activity. [...] However, the discussion in not completely satisfying because a mixed effect of phase resetting and an increase of induced activity cannot be excluded. [...] Overall, the results tend to support the hypothesis of separate neural oscillations, in addition to ongoing brain activity, as the generation mechanism of the ASSR.”

In a second experiment, the periodicity of the 40 Hz AM sound, which was used to elicit the ASSR, was perturbed by a 180° phase shift. This perturbation in the periodicity of the AM stimulus itself caused an ASSR desynchronization that was similar to that observed with an additional noise burst. The ASSR phase followed the phase shift in the stimulus. All in all, a rather general change detection can cause an ASSR reset. This is of interest in the context of this survey, as motor vehicle vibrations are intrinsically noisy, and decoherence of ongoing vibrations is likely observable at

Figure 7: Examples of 40 Hz ASSR phase distribution in a pre-stimulus interval (-10 ms), after ASSR onset (230 ms), during stimulus induced perturbation (470 ms) and after recovered ASSR (630 ms). Copied from [2].
various frequencies. It is hard to generalize the effects of a short noise burst or other perturbation to the case of long lasting perturbations, and clearly further experimental evidence is needed. Nevertheless, the findings of this study along with the identification of stochastic resonance in the somatosensory system (see subsection 4.9 below) could be useful for a start.
3. Visual Modulation of Neural Oscillations

Steady-state visual evoked response (SSVER\textsuperscript{3}) is another interesting neurophysiological phenomenon. It is analogous to but different than ASSR. Rhythmical visual stimuli in the 1-100 Hz frequency range evoke a phase-locked oscillatory response in the human visual cortex [74,77]. Prominent responses are also observed at harmonics of the stimulus frequency, in both humans and cats [74]. A prominent enhancement of alpha activity by a wide range of stimulus frequencies was observed in humans [74,76-7], but not in cats [74]. A rhythmical visual stimulus at \textasciitilde 40 Hz elicits a unique response [74,77] that is reflected in cognitive performance [78-9]. The precise mechanisms that underlie SSVER and its interaction with ongoing neural activity are yet unknown [76-7,86].

3.1. Response Frequencies vs. Stimulus Frequency – Christoph Herrmann [74] has taken EEG recordings of the visual cortices of ten adult subjects exposed to flicker stimuli. He painstakingly probed the 1-100 Hz frequency range in 1 Hz steps, extracting the stimulus-phase-locked components of the EEG frequency spectra. A surface plot was produced of the EEG grand-averaged evoked response frequencies as a function of stimulus frequency, which is worth more than a thousand words. For consistency and convenience, I've flipped its axes:

\textsuperscript{3}In the context of EEG evoked potentials, SSVER is also called SSVEP [74,86] or photic driving [76].

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure8.png}
\caption{SSVER frequencies as a function of stimulation frequency. Adapted from [74].}
\end{figure}
The diagonal along the fundamental stimulus frequency indicates that the visual cortex is driven by the flickering stimulus at precisely its frequency. In addition, several weaker harmonics are visible up to rather high response frequencies. A subharmonic diagonal is visible at the alpha frequency range, indicating that ~10 Hz alpha activity is also evoked by higher frequencies, especially by its harmonics (note enhancement of 10 Hz activity by 80 Hz stimulus).

The response to 39 Hz stimulus is unique – numerous response peaks are observed at frequencies which are all multiples of 13.5 Hz. The fundamental response frequency is shifted from 39 Hz to 40.5 Hz (third multiple of 13.5 Hz). The 13.5, 40.5 and 54 Hz response peaks are relatively consistent among different subjects, whereas larger inter-individual differences are found in the frequency of the ~27 Hz response and higher harmonics.

The 50 Hz response peak is mainly an artifact of the local line frequency, but its peaks are observed for flicker stimuli of 1, 5, 10, 25, 50, 75 and 100 Hz. This suggests that the line frequency offset gave expression to sub-threshold evoked responses, at frequencies which are in harmonic relation to 50 Hz.

Reproduced in [74] is a similar surface plot, based on local field potentials and recordings of multi unit activity from area 17 of cat visual cortex. A strong response is clearly observed at the stimuli frequencies, and their first two harmonics. While a stronger response is observed for flicker stimulus of the 2-10 Hz range, there is no apparent enhancement of alpha activity during higher stimulus frequencies. This is in stark contrast to the enhancement of alpha activity in humans by multiple stimulus frequencies in the 1-100 Hz frequency range, evident in figure 8.

3.2. SSVER and Pre-Stimulus Activity – The nearly continuous diagonals observed in figure 8 are the result of averaging over all subjects. For any individual subject, there's only one spectral peak per frequency range along the diagonal – one at ~10 Hz, one at ~20 Hz and one at ~40 Hz. In other words, SSVER amplitude is highest for a specific stimulus frequency, a so-called 'preferred resonant frequency' [76], which is different for each subject, as evident in figure 9.

Some studies have suggested that this preferred resonant frequency depends on its proximity to the spontaneous alpha peak frequency [76]. However, a recent study [76] found that the correlation between the two was not statistically significant. This lack of correlation is exhibited even among those subjects whose dominant pre-stimulus frequency coincided with one of the stimuli frequencies [76]. Nevertheless, undriven alpha activity is suppressed during rhythmical visual stimuli, and its degree of desynchronization is positively correlated with the amplitudes of the evoked responses at the stimulus frequency and its harmonics [76]. This suppression is demonstrated in figure 10.

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A single recent study [86] has reported a significantly stronger SSVER in females than in males, in terms of both spectral power and phase-locking. As evident in the figure 11, males and females exhibit a similar temporal pattern of phase-locking to a 18 Hz flicker, to different extents. Phase-locking factor for a 25 Hz flicker was smaller by ~0.15, exhibiting similar gender difference and temporal pattern. As females also exhibit an increased resting EEG, these findings suggest a linkage between pre-stimulus activity and SSVER. According to the authors, whether a similar gender difference exists in the auditory modality is currently unknown.

3.3. 5 Hz Stimulus Enhances Alpha Activity – Pastor et al. [77] investigated SSVER using EEG and PET, in a procedure resembling their ASSR study [3], reviewed in section 2.1 above. The stimuli were white flashes presented binocularly at 14 frequencies in the 5-60 Hz range.

According to the authors, an oscillatory EEG response, phase-locked with the presented flash frequency, was elicited by all stimuli frequencies. Greatest SSVER amplitudes at stimulus frequency were recorded for ~15 Hz stimulus in the occipital area and for 25 Hz stimulus in frontal areas. This result is somewhat misleading though, as the 5 Hz clearly elicited strong responses at its 10 Hz and 15 Hz harmonics, that are not taken into account by the authors, despite their clear appearance in the 5 Hz SSVER spectra (see figure 12). The peaks at 10 Hz and 15 Hz are easily identified by comparing the 5 Hz SSVER spectrum to those for 10 Hz and 15 Hz.

The PET study revealed that the regional cerebral blood flow (rCBF) increased in visual primary and association areas (Brodmann areas 17, 18, 19) for all the probed stimulation frequencies (5, 10, 15, 25 and 40 Hz). The highest local increase in rCBF was observed for 5 Hz stimulus. An earlier study found highest rCBF increase for 7-8 Hz stimulation rate, leading the authors to explain the maximal response at 5 Hz by its proximity to the unprobed 7-8 Hz.

The discrepancy between the EEG 15 Hz peak and the rCBF 5 Hz peak was resolved by the authors by weighting the rCBF data by the SSVER amplitude. According to the authors, this weighting illustrates

![Figure 11: Mean phase locking factor values during 18 Hz flicker stimulation for each gender at Oz electrode site. Copied from [86].](image)

![Figure 12: Top - SSVERs at O2 electrode site (left) and their spectrograms (right). Bottom - SSVER at stimulation frequency, averaged over three occipital electrode sites (Oz,O1,O2). Copied from [77].](image)
the correlation between the EEG response and changes in rCBF. The weighted activation was localized to a smaller area in Brodmann area 17, whose shape and orientation “follow the outline of the calcarine sulcus”. This region “encompasses the cortical representation of both the peripheral retina and the macular region”. The authors thus suggested the SSVER increased amplitude at stimulus frequency corresponds to a true activation of neuronal clusters in the primary visual cortex.

However, the discrepancy between the EEG and rCBF preferential frequencies may originate from the authors' method of taking into account only the SSVER amplitude at the stimulus frequency. Taking into account the total increase in EEG power during stimulus would have resulted in higher values for the 5 Hz stimulus, possibly matching the rCBF results.

In an earlier study, Mori & Kai [95] clearly demonstrated the entrainment of ~10 Hz alpha activity by 5 Hz flicker stimuli delivered with eyes closed. The authors remark that entrainment of alpha activity with a 10 Hz stimulus is “usually most predominant but often influenced by the subject's mental and physical condition (e.g., stress) at the moment of testing, while harmonic entrainment is rather insensitive to such uncontrollable factors.”

In the context of this survey, these studies provide evidence for the enhancement of 10 and 15 Hz alpha activity by a subharmonic 5 Hz visual stimulus. These findings are of interest as a similar alpha enhancement is suggestively observable in the somatosensory response to vibrotactile stimuli (see section 5.2 below).

3.4. Visual Hallucinations During Alpha SSVER - According to Herrmann [74], the strong alpha band response to 10-15 Hz flicker stimuli, visible in figure 8, was accompanied by the perception of hallucinations. In Herrmann's words: “Most subjects reported form (stars or stripes) and color (blue, red or purple) illusions at frequencies around 10-15 Hz. […] The observed hallucinations could be due to oscillating SSVEP propagating across retinotopic areas of visual cortex. One area then is successively excited and inhibited, thus leading to hallucinations. This phenomenon is known from certain kinds of epilepsies and has been simulated in mathematical models (Tass 1995, 1997 [85 LG]). Some of our subjects were retrospectively shown the hallucinations by Tass (1995) and reported them to be identical to the ones observed.”

Pastor et al. [77] have not reported whether their subjects experienced hallucinations. Nevertheless, they have measured increased cerebellar activity during 5 Hz stimulus, and less significantly during 10 Hz stimulus. This was interpreted by the authors as participation of the cerebellum in visual processing. In their earlier ASSR study [3], a similar cerebellar activation during 40 Hz auditory stimulation was attributed to the inhibitory role of the cerebellum. Suggestively, the cerebellum becomes more active to inhibit excessive cortical firing elicited by the 40 Hz auditory stimulation (see section 2.1). A similar explanation may be useful here. As explained by Peter Tass [85], visual hallucinations correspond to either traveling or standing waves of cortical activity. These waves arise when the mutual interactions between excitatory and inhibitory neuronal populations are too strong with respect to their self-interactions (excitatory-excitatory and inhibitory-inhibitory). This oscillatory instability is normally useless and possibly unfavorable to the ordinary operation of the visual system. Therefore, cerebellar inhibitory activity may be of use in down-regulating this response. This explanation may be tested by (carefully) exposing subjects whose cerebellar activity is defective or suppressed, to 5-15 Hz flicker stimuli.

3.5. Uniqueness of 40 Hz SSVER – As noted above, Herrmann [74] reported a unique response to 39 Hz flicker stimulus. Numerous response peaks were observed at frequencies which are all multiples of 13.5 Hz, including a significant response at 40.5 Hz rather than 39 Hz. Accordingly, the pattern of rCBF activation by 40 Hz stimulus revealed by Pastor et al. is denoted as 'remarkable' [77]. The 40
Hz stimulus activated only the primary and association cortex representing the macular region of the retina, whereas stimuli at other frequencies also activated those regions representing the peripheral retina. Citing from [77]: “This region participates in tasks such as reading, which requires a greater interaction with Wernicke's area and other cortical structures involved in this task. […] Isolated macular cortex activation by 40 Hz probably reflects the specific activation of the retinal cones represented in this cortical region and lack of activation of the rods of the peripheral retina by stimulation at frequencies of > 30 Hz, a phenomenon well documented by electroretinography”. ~30 Hz is known as the 'flicker fusion frequency', above which the flicker stimuli is perceived as a constant dim light [74]. As no other frequencies above 30 Hz were probed by Pastor et al. [77], it is unclear whether their reported macular-only response is common to all stimulus frequencies above 30 Hz, or unique to 40 Hz.

3.6. Cognitive Performance Reflects SSVER – In a series of studies from 1998 and on, Elliott and Müller demonstrated that a flickering 40 Hz visual stimulus may prime the detection of a subsequent illusory visual object [78-9]. A Kanizsa-type illusory square, composed of four 90° corner elements (├), served as a target presented within a 3X3 matrix of distractor corner elements. Prior to target display, observers were presented with a pre-mask display of a 3X3 matrix of flickering crosses. The pre-mask display involved the repeated presentation of four image frames, each consisting of 1-4 crosses that were repeatedly presented at a fixed location within the 3X3 matrix. One of the pre-mask frames consisted of four crosses, whose locations differed between the 'synchronous' and 'random' experimental conditions. In the 'synchronous' condition, on target-present trials, the four crosses occupied the same locations as the following Kanizsa-type square. In the 'random' condition, the four crosses were presented in pseudo-random arrangement that did not correspond to a square.

The mean reaction time (RT) widely varied between experiments in the ~480-730 ms range, yet was consistently longer by ~70 ms for target-absent trials than for target-present trials, similarly for 'synchronous' and 'random' conditions. This finding suggests large inter-individual differences in additive latencies (motor action latency etc.) and a conserved frame scanning time. Importantly, the mean RT for target-present trials was significantly shorter for 'synchronous' than for 'random' conditions, suggesting a priming effect upon some kind of a visual working memory. This 'synchrony priming' was obtained despite the proven inability to consciously detect the presence of a synchronous pre-mask frame. This priming effect exhibited spatial specificity - it was confined to targets presented at the location of the synchronous pre-mask frame. A maximal reduction of RT by ~40 ms was achieved when the pre-mask frames were alternated at a rate of 40 Hz, and presented at a 180° phase shift with respect to the target stimuli. The minimal priming duration required was two full cycles of four sequential pre-mask frames (200 ms), with an indistinguishable effect for longer priming durations. The perception of Kanizsa-type illusory shapes necessitates the binding of distinct visual elements, which was shown in numerous studies to be associated with an increase in synchronous 40 Hz gamma activity over numerous brain regions (see for instance [80-82,120]). Therefore it is only natural to suggest the existence of some kind of an oscillatory visual working memory, which maintains information about the figure-ground organization of the visual field, for a very brief period of time. According to this assumption, the pre-mask frames, alternating at 40 Hz, modulate the firing rates of visuo-cortical neurons, thereby entraining this oscillatory working memory. This suggested mechanism is discussed in length in [78-9].

However, EEG recordings reveal a more puzzling neural response, as reported in [79]. In this study, twelve subjects preformed the said detection task while undergoing EEG recordings. A synchronous evoked response was prominent under occipital (O1 and P3) and prefrontal (Fp1) electrode sites. The
A spectrogram representing the time-frequency decomposition of the average component activation is hereby pasted:

![Spectrogram](image)

Surprisingly, no sustained activation at ~40 Hz or any other frequency band is observed at any time in the EEG spectrogram. Instead, activity at a number of frequencies is observed, shifting downwards in frequency with time. Quantitatively, diagonal bands of activation appear with a periodicity of ~200 ms (~5 Hz) and a slope of -160 Hz/sec. Other studies have reported a downward shift in frequency with time, in the EEG evoked suppression response to visual [75] and tactile [59] stimuli, yet this diagonal pattern arguably remains unresolved by present literature.

The authors analyze in length the spectral activation peaks exhibited in the EEG spectrogram, during a specific time interval (341 ± 29 ms into the presentation of the priming pre-mask frames). This time interval seemingly bears no special importance, nor a unique pattern of neural activation. The authors suggestively accommodate the observed EEG spectrogram into their 40 Hz oscillatory visual working memory paradigm, despite the apparent absence of sustained 40 Hz neural activity.

Summing up, Elliott and Müller convincingly demonstrated that a rhythmical 40 Hz visual stimulus may prime the detection of a subsequent illusory visual object. This priming effect is sensitive to frequency, phase and location, in concordance with the entrainment of oscillatory neural activity by the priming stimulus. Nevertheless, EEG measurements provide no evidence for such entrainment, revealing instead an intriguing diagonal spectral pattern of neural activity. Importantly, both occipital and prefrontal sites appear to be involved in the formation of the prime response, indicating that rhythmical visual stimuli may have widespread effects on neural activity, not entirely localized to the visual cortex. Future research may reveal the extent to which this prefrontal activity is modulated by attention.

3.7. Supporting Pseudo-Scientific Testimonies – As in the auditory case (see section 2.4), there is at least one commercial firm, Mind Alive Inc. ([http://www.mindalive.com/](http://www.mindalive.com/)), that sells pseudo-scientific audio-visual products based on ASSR and SSVER. According to the company website, their...
products “assist in reducing the symptoms of Stress and Anxiety, Post Traumatic Stress Disorder (PTSD), Attention Deficit Disorder (ADD), Pre-Menstrual Syndrome (PMS), Chronic Fatigue Syndrome (CFS), Seasonal Affective Disorder (SAD), Depression, Insomnia, Autism, Chronic Pain and Fibromyalgia.”

Once again, if these products are indeed more effective than placebo, regardless of their credibility, it may support the hypothesis that entrainment of whole brain activity by audiovisual stimuli is not limited to the auditory and visual cortices. However, the testimonies brought in the company website describe various dramatic effects on cognition and health, whereas all the scientific literature I have found does not report any dramatic effect by any kind of mild sensual stimuli (except prolonged sensual deprivation). The only possibly dramatic effect that is widely reported, studied [85] and replicated is the visual hallucinations elicited by 10-15 Hz flickering, as described in subsection 3.4 above.
4. The Somatosensory System – Responsiveness & Rhythms

In contrast to the abundant literature investigating brain response to rhythmical auditory or visual stimuli, I have only found fifteen EEG\MEG studies dealing with human brain frequency response to rhythmical vibrotactile stimuli. The context of their findings was elucidated by the conclusions of other neuroscientific somatosensory studies, cited as follows. The fifteen vibrotactile EEG\MEG studies are reviewed in the next section.

4.1. Cerebral Areas Involved in Somatosensory Processing – For a start, we shall briefly denote the different brain areas involved in somatosensory processing, as elaborated in the following subsections.

The post-central gyrus, also known as the primary somatosensory cortex (SI), includes Brodmann areas 3a, 3b, 1 and 2 [173,176]. It responds within 20-35 ms to contralateral somatosensory stimuli, during wakefulness and sleep [174].

The parietal operculum, also known as the secondary somatosensory cortex (SII), lies deep within and along the upper bank of the Sylvian fissure [173-4,176]. Direct cortical stimulation of the human SII cortex produces percepts such as a 'desire to move' and an 'incapacity to move', whereas the percepts of phantom limbs in amputated patients were associated with decreased SII EEG activity [174]. It responds within ~70 ms to both contralateral and ipsilateral somatosensory stimulation. Its response amplitude increases with attention [38,40,174,177].

The parietal association area, also known as the posterior parietal cortex (PPC), is involved in the integration of sensory and motor processing, as well as the combination of tactile and proprioceptive information with other sensory modalities [174]. PPC is rather multi-modal, as PPC neurons may be activated by cutaneous, kinesthetic and visual stimuli [176]. Its response is weaker and less consistent than those of SI and SII cortices, thus it's unclear whether its relative absence in neglect patients indicates a linkage to the underlying mechanism of the neglect syndrome [175].

Two MEG studies have also reported the involvement of the mesial cortex of the paracentral lobule, in somatosensory processing [171,174]. Its relatively weak response was even weaker or absent for unattended stimuli [171]. Another MEG study reported a delayed bilateral activation of the premotor frontal cortex, in the ~70-200 ms interval after the median nerve is electrically stimulated [172-3].

Speaking of latencies, contralateral SI activation precedes the bilateral activation of SII cortices, as well as the contralateral PPC, by ~50 ms. The observed latency in SII activation does not necessarily imply a serial processing of somatosensory information, via the SI to SII cortex, since the SII cortex also receives direct thalamic input [174]. The importance of the thalamic pathways has remained uncertain and the serial [172-3] vs. parallel [174-5] processing of somatosensory information between the SI and SII cortices has been under debate. Moreover, the ipsilateral SII cortex is not necessarily dependent on activation of the contralateral SII, which could come of use in case of lesions or other trauma [175].
4.2. Monkey Cortical Activity During Vibrotactile Stimuli – Ranulfo Romo's group [9-16] trained monkeys to compare the frequencies of two mechanical vibrations applied sequentially to the tip of a finger, and to report which of the two stimuli had the higher frequency. This task requires encoding the first stimulus frequency, maintaining it in working memory, encoding the second frequency, comparing it with the memory trace that was kept of the first stimulus, and reaching a decision that has to be communicated to the motor system. Single neuronal activity was recorded through movable microelectrodes, inserted in parallel into various sites in the primary somatosensory cortex (SI), secondary somatosensory cortex (SII), prefrontal cortex (PFC) and medial premotor cortex (MPC) of several trained macaque monkeys. This ~10 year research shed light on some of the mechanisms involved in paying attention to the stimulus, encoding its frequency, storing it in working memory, comparing the two stimuli and carrying out the desired motor movement. An enlightening 2003 review [9] summarizes the outcomes of this research (up to its compilation date). A later paper [14] reported that the firing rate of a population of PFC neurons was correlated with the behavior of the monkey, suggesting their activity as part of the neural substrate of working memory during the task.

I will now focus on the findings relevant to this survey.

There are various differences between SI and SII activity during flutter frequency discrimination. SI firing rates usually increase with increasing stimulus frequency, but just a small fraction of all responsive neurons show strong frequency modulation [9,13]. The timing of SI spikes reflected very precisely the periodicity of the stimuli, or its temporal pattern in the case of aperiodic stimuli. However, while significant covariations were found between the evoked firing rates and the psychophysical response, no such association was found between the spike timing and the psychophysical response. Periodic and aperiodic stimuli evoked almost the same modulations in firing rate, with the monkeys unexpectedly reaching a similar level of performance for aperiodic stimuli within a few trials. Thus stimulus frequency is apparently encoded through a mean-rate code [9,13], suggestively weighted in a manner reproducible by multiplying the spike count by a weighted window that has most of its mass in the first 250 ms [15]. There is no indication that the high periodicity that the flutter elicits in SI contributes to frequency discrimination in this task, though this temporal information could be used for other purposes, such as the perception of surface roughness [9]. Evoked spikes in SI were more phase-locked to the stimulus during active discrimination than during passive discrimination, with appreciable reduction in periodicity in SI Brodmann area 1 compared to area 3b, and almost no periodicity in SII [13].

Interestingly, the monkeys performed the discrimination task just as well when the vibrotactile stimulus was replaced by intra-cortical microstimulation of clusters of rapidly-adapting neurons in area 3b of SI cortex. Apparently, neural input of the same fundamental frequency as the vibrotactile stimulus is sufficient for frequency discrimination. Consequently, one may assert that a given rhythmical vibrotactile stimulus is predominantly encoded by its fundamental frequency, at least in SI cortex. This convenient assertion is non-trivial, as different coding mechanisms are found in other somatosensory systems. For instance, when a rat whisker is vibrated, the neural firing frequency recorded in its barrel cortex is proportional to the mean velocity of the vibration (amplitude times frequency), and not to its frequency [196].

Neurons in SII show complex somatosensory responses and are known to be modulated by attention [10]. SII is connected to many cortical areas and is thus suitably placed to integrate both sensory and memory information. In the context of the frequency discrimination task, the neuronal responses of

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4 This finding is corroborated by another study, irrelevant for this survey, available at: http://dx.doi.org/10.1152/jn.01002.2003

5 More precisely, spiking of some specific neurons identified in the primary somatosensory cortex [13].
SII allowed a particularly straightforward interpretation [10]. The characteristic population response gradually became dominated by responses that were a function of the frequency difference (f2-f1), as evident in figure 14:

Figure 14: Population dynamics in four cortical areas during the discrimination task. Each data point represents one neuron. For each neuron, responses were fitted to the equation: firing rate = a1f1 + a2f2 + b, where f1,f2 are the vibrational stimuli frequencies, and a1,a2 and b are coefficients. For instance, points on the a1=0 axis represent responses that depend on f2 only, whereas points on the a2 = -a1 line represent responses that are functions of f2-f1. Scanned from [9].
As noted by the authors, it is tempting to interpret this strikingly simple SII response as being itself involved in the formation of the choice. However, recordings in the MPC and PFC during the same task have shown that choice-correlated responses arise in these cortices earlier than in SII. It is therefore unclear whether SII neurons directly participate in forming the choice itself, or merely reflect the result of a choice formed elsewhere. The authors speculate that information about the base frequency $f_1$ is fed back to SII neurons from higher areas, such as the PFC, in a manner analogous to that in which the PFC can feed information back to the inferotemporal cortex in visual tasks.

Relevant neurons in SI were active only during stimulation, and most of them increased their firing rates with increasing stimulus frequency. In the other cortices, most significantly in PFC, delayed activity is evident throughout the inter-stimulus period, with both firing rates that increase and decrease as function of base frequency $f_1$. These temporal dynamics are demonstrated in figure 15:

![Figure 15: Neuronal responses evoked by the base stimulus in four cortical areas during the discrimination task. Left – Spike density functions from four single neurons. Dark bars above each plot indicate times during which the neuron's firing rate carried a significant monotonic signal about the base stimulus. Right – Numbers of recorded neurons carrying a significant signal about the base stimulus, as a function of time relative to the beginning of the delay period. Scanned from [9].](image)

Upon arrival of $f_2$ stimulus, neurons in all three cortices (SII, PFC and MPC) cluster around the line $a_2 = -a_1$, corresponding to firing rates proportional to ($f_2-f_1$), as evident in figure 14. The sustained modulation in SII activity during the inter-stimulus period was greatly reduced during passive stimulation [13], and correspondingly no dependence on either $f_1$ or $f_2$ was recorded in SII in the task + lights variant in which the vibrotactile stimulus was irrelevant [10]. The temporal response dynamics of SII are further analyzed in [9,10] in a level of depth irrelevant for this survey.
These findings argue against the participation of SI neurons in maintaining the frequency of a given stimulus in working memory (see figure 15 top). Studies performed by Zhou & Fuster with rhesus monkeys lead to an opposing conclusion [178-9]. These studies showed that SI neurons can also be involved in retaining visual [178] and auditory [179] information, that has been associated with the touch of an object. Whether the discrepancy stems from differences in training, brain anatomy or measurement techniques will hopefully be resolved in the near future.

Some of Romo et al.'s findings were replicated in humans [38,40,66,70,72,172-4,177]. I have found no human studies conflicting with their findings, but my search has not been exhaustive.

4.3. Synchronous Oscillations in the Alpha Range – Alpha Rhythms are found in many regions of the brain and may be generated by a number of potentially different mechanisms [61]. According to computational studies [60,61], alpha rhythms can be sustained at frequencies of 7-14 Hz for physiologically realistic parameter values. While synchronous beta and gamma oscillations can be sustained over long cortical distances, synchronous alpha activity is only stable for short coupling delays, corresponding to local oscillatory networks [60,61]. It should be noted however, that synchronous gamma rhythms at low frequencies such as 8 Hz were shown to be robust in carefully tuned networks, according to a recent study [62]. I find it hard to estimate the applicability of this recent computational prediction to in vivo studies, yet it is tempting to ascribe synchronous cortical 8 Hz activity [4,190-2] to such low-frequency gamma rhythms.

The abundance of local alpha rhythms has lead to association of several different terms with local oscillatory activity observed in the somatosensory and motor cortices. In the Rolandic cortex, 7-14 Hz oscillations lasting for 0.5-2 seconds at a time are identified as the 'mu rhythm', a term sometimes also used referring to Rolandic activity at about 20 Hz [29,36,64,65]. This could easily be misleading, as the source of the 7-14 Hz mu rhythm is localized in the primary somatosensory area, whereas the 20 Hz beta rhythm is generated in the motor cortices [29,43,45,64,176, but see 49]. It should thus be emphasized that the 10 Hz and 20 Hz rhythms seem to have different sources and reactivity, probably serving different functions. In the present work, mu rhythm refers to 7-14 Hz activity recorded over central sites.

7-9 Hz activity in the secondary somatosensory cortex is called 'sigma rhythm' [7,8], while a similar 8-10 Hz alpha activity close to the auditory cortices is called 'tau rhythm' [64,65,125]. The mean frequency of the occipital ('classical') alpha rhythm is lower than that of the Rolandoic mu rhythm, by 0.6 Hz [126] to 0.9 Hz (9.6±0.7 Hz vs. 10.5±0.9 Hz) [36]. Accordingly, the term mu rhythm was sometimes used interchangeably with 'upper alpha' in the 10-13 Hz, which is distinguished from 'lower alpha' activity in the 7-10 Hz band [29,35,36,114]. This 7-10 Hz lower alpha definition partially overlaps with the definition of 4-8 Hz as theta band, sometimes divided in itself into 4-6 Hz 'slow theta' and 6-8 Hz 'fast theta' [34]. Adding to the confusing nomenclature [64] are large inter-individual differences of all rhythms in the alpha frequency band [29,40,70,74].

4.4. Event-Related (De)-Synchronization – There's a rather large body of work investigating event-related synchronization and desynchronization. Its underlying assumption is that a sensory stimulus elicits an evoked activity within a roughly fixed time-delay, whereas ongoing neural activity behaves as additive noise [29]. This basic assumption has been intensely debated in recent years [75,58,59,83,84]. Even an 1999 review article on event-related synchronization [29] opens with a clarification that this assumption does not hold in general. Nevertheless, some important revelations were made using this outdated assumption, which will be reviewed in this subsection. The following subsections will cover more recent findings that complement, supersede and reinterpret the findings reviewed here.
A voluntary hand movement results in a desynchronization of the 10-13 Hz upper alpha and 20-24 Hz beta band activity, localized close to sensorimotor areas [29,114]. This event-related desynchronization (ERD) starts about two seconds prior to movement-onset over the contralateral Rolandic region and becomes bilaterally symmetrical immediately before execution of movement. Similarly, a voluntary foot movement results in a desynchronization in the 7-8 Hz band as well as in the 20-24 Hz beta band [29]. The local desynchronization of alpha rhythm may be accompanied by an increase in synchronization in neighboring cortical areas that correspond to the same or another modality. For instance, a hand movement often results in a hand area evoked desynchronization and simultaneously in a foot are synchronization, with an opposite pattern elicited by foot movement [29,30,114]. This phenomenon, termed “focal ERD/surround ERS”, is interpreted as inhibition of surrounding sensory cortical areas in response to local stimuli. This interpretation is supported by regional cerebral blood flow (rCBF) measurements, showing a decrease in rCBF in the somatosensory cortical representation area of one body part (e.g. hand area) whenever attention is directed to a distant body part (e.g. foot area) [30].

Mu rhythm ERD may also be elicited by tactile [43,45,47] or painful [54] stimuli. Pain globally suppresses all alpha band rhythms - both the Rolandic mu rhythm and the occipital alpha rhythm - with mu suppression more significant in the right hemisphere, regardless of stimulus handedness [54]. A tactile stimulus elicits mu rhythm suppression in the contralateral somatosensory cortices [43,45,47], during either wakefulness or REM sleep [47]. Its precise locations are pointed out in [43,45].

Induced beta oscillations (at 14, 19 and 23 Hz in different subjects) are found in the first second after termination of a voluntary movement, when the Rolandic mu rhythm still displays a desynchronized pattern of low amplitude [29]. The mean frequency of the induced beta activity is roughly the same for tactile stimuli delivered to different fingers, with much larger inter-individual differences in the mean frequency of the induced beta activity [44] (the 3 subjects in the reported experiment exhibited induction of beta activity at ~16, ~18 and ~22 Hz).

Induced gamma oscillations at around 40 Hz are also found, reaching maximal power shortly before movement onset [29]. Increased synchrony of 40-46 Hz gamma activity has also been observed in the contralateral primary somatosensory cortex (SI), following electrical stimulation of the thumb, but not the little finger [69]. As synchronous gamma oscillations can be sustained over long cortical distances [61], their event-related synchronization in the somatosensory cortices prior to movement was explained as reflecting binding of information between spatially separated cell assemblies [29]. A later review article [120] argued against this information binding paradigm, suggesting instead that synchronized gamma band activity is involved in the representation of cognitive functions.
4.5. Imaginary Movements and (De)-Synchronization –Interestingly, both pre-movement desynchronization and post-movement synchronization are similarly observed when the subjects are asked to observe or imagine a movement instead of actually performing it [29,30,36]. This is analogous to the suppression of posterior ~10 Hz alpha activity similarly by either visual stimulus or mental imagery [64]. Based on motor imagery, subjects can learn to control suppressions and enhancements of the mu rhythm, within several hours of training [36]. Focal ERD/surround ERS following imagined movement of different body parts are demonstrated in the figure 16.

The clearest similarity was observed for imagined hand movements, with more puzzling responses observed to imagined foot or tongue movement [30]. Note synchronization \ desynchronization of 33 Hz activity at electrode positions C3 and C4, which are close to the primary somatosensory cortices. I have found one other human study [70] reporting 28-32 Hz activity in the primary somatosensory cortex, but none explaining its functional role.

It has been suggested that mu desynchronization in response to observed and imagined movements plays a critical role in imitation learning, or the ability to understand others' movements [36].

4.6. Somatosensory Phase Locking Following Tactile Stimuli – An exceptionally elegant paper by Simões et al. [49] reports that activity in human primary and secondary somatosensory cortices is phase locked by ~20 Hz beta oscillations. In this MEG study, electric pulses were delivered once every three seconds to the right median nerve of ten subjects. In agreement with previous studies, the earliest response to the stimulus was located in the contralateral (left) SI cortex, reaching an activation peak within 22 ms of stimulus onset. This was followed by activation of the left and right SII areas, peaking at 82 and 92 ms of stimulus onset, respectively. Phase locking between the left and right SII

![Figure 16: Time-frequency maps (top) and topographical distributions (bottom) of event-related activity during motor imagery tasks. Copied from [30].](image-url)
areas was found at frequencies of 18-22 Hz during the interval of 80-110 ms of stimulus onset. The phase locking was statistically significant in 9 of 10 subjects between 15 and 25 Hz, and clearly absent over the scalp midline. Importantly, a substantial part of the phase locking between left SI and right SII cortices was not time-locked to the stimuli. This was taken as evidence for an intrinsic interaction within the somatosensory network, whose exact origin and mechanism is presently unknown.

My untrained eye spots a similar phase locking at about ~10-12 Hz between the same sites during the same time intervals as the phase-locking at 18-22 Hz (see figure 17). Moreover, the non-stimulus-locked 18-22 Hz mostly occurs during the ~50-120 ms time interval, whereas the weaker non-time-locked 10-12 Hz activity occurs during the ~350-420 interval. These findings are especially intriguing as earlier literature [36,68] has attributed a lack of bilateral coherence to the Rolandic mu rhythm. I have no idea why these findings aren't discussed or explicitly rejected by Simões et al. [49], but a similar synchronization in the alpha band is reported in subsequent studies [39,58,59] (see following). This observation may be taken as evidence for phase-locking in the alpha band between the somatosensory cortices. Alternatively, it may be interpreted as a global increase in alpha synchronization some 300 ms after stimulus onset. Further data analysis of the experimental data collected by Simões et al. could tell the two possible phenomena apart.

Computational studies explicitly demonstrate how a given neural network can undergo transitions between alpha, beta and gamma rhythms as arousal increases [61]. Jensen et al. [67] have specifically shown how sensorimotor 15-30 Hz beta oscillations can arise in a simulated neural network of 20 excitatory and 8 inhibitory Hodgkin-Huxley type model neurons with all-to-all connections. During gamma oscillations, both excitatory and inhibitory neurons fire on every cycle. During beta oscillations, inhibitory neurons fire at gamma frequencies while excitatory neurons fire on every other inhibitory neuron cycle. Since the excitatory neurons skip the same cycles, the population firing rate reflects their lower firing rate, of about 20 Hz in the beta range [61,67].

4.7. Somatosensory Phase Locking and Perception – In a later MEG study, Palva et al. [58] delivered weak electric pulses to the index fingertips of fourteen subjects. The stimulus intensity was adjusted so that no more than half of the trials were reportedly perceived. All stimuli were followed by a clear and prolonged suppression at the alpha, beta and gamma frequency bands. In all brain regions, these amplitude decreases were larger for the perceived than for the unperceived stimuli. In the contralateral SI cortex, phase locking to the perceived stimuli was observed at all frequency bands probed in this study (4-45 Hz). However, in the contralateral SII cortex, no gamma band stimulus locking was observed. Furthermore, in the ipsilateral SI and SII cortices, only theta (4-7 Hz) and alpha (8.5-15 Hz) band stimulus locking were significant. This ipsilateral phase locking reached significance during the interval of ~160-300 ms of stimulus onset. Importantly, significant phase locking to unperceived stimuli was only significant in the contralateral SI cortex, and only in the theta and beta (15-26 Hz) frequency bands. This finding is compatible with an earlier finding, cited in [120], of 30-50 Hz gamma band coherence observed in the contralateral SI cortex, ~150-300 ms after a perceived but not a nonperceived hand stimulus.
Stimulus locking in the alpha band also extended to frontal and parietal regions, significantly during the 80-150 ms time interval of perceived stimulus onset. Bearing in mind the prominence of synchronous alpha oscillations during working memory tasks [193-5], this finding is taken as evidence for the formation of a sensori-fronto-parietal network employed for conscious processing of the perceived stimulus. Thus what was previously identified as 'mu rhythm ERD', is now reinterpreted as an increase in synchronous alpha oscillations, that may be involved in higher cognitive functions.

Interestingly, no induced (i.e. non-stimulus-locked) beta or gamma band activity was observed in this study. This is in stark contrast to the findings reported by Simões et al. [49]. Thus, Palva et al. [58] reproduce the bilateral phase-locking of somatosensory cortices in the alpha band, shown but not mentioned in [49], but do not reproduce the similar phase locking in the beta band shown and discussed in [49]. The longer latencies observed by Palva et al. [58] with respect to [49] may be explained by the delivery of tactile stimuli to the hand, instead of electrical stimuli to the median nerve. Other discrepancies may be resolved by later studies.

Palva et al. [58] also argued that “neural activity in the prestimulus period contributes to the "perceptual fate" of the stimuli”. This is in line with a previous paper of the same group [57], which suggested that prestimulus neural activity in the somatosensory cortex was correlated with the probability of perceiving the near-threshold stimuli. However, a recent study in monkeys [16] have found no correlation between the prestimulus activity of SI neurons and the probability of stimulus perception. Instead, such a correlation was found between the activity of neurons in the frontal lobe and the monkeys' probability of stimulus perception.

4.8. Widespread Phase Locking and Attention – Bauer et al. [59] recently used Braille stimulators to present dot patterns to the index fingers of nine healthy (sighted) subjects. Dot patterns were presented to both index fingers, while the subjects were instructed to report the reoccurrence of an initially presented sample pattern at one side (finger), ignoring the unattended side. Thus this MEG study included both attended and unattended, matching and non-matching stimuli.

A first brain response peaked ~50 ms after stimulus onset in the contralateral SI cortex, followed within ~30 ms by a contralateral SII activation. These latencies are in accordance with those reported in previous studies [49,58]. Bilateral activation of somatosensory areas began ~120 ms after stimulus onset and sustained for at least ~500 ms, accompanied by activation of lateral parietal regions. Within ~300 ms of stimulus onset, a new cluster of evoked activity was observed in the medial occipital cortex. There was no consistent attentional modulation of this evoked component, in contrast to the strong attentional modulation of the stimulus-induced occipital activity, described hereunder.

The most prominent effect of tactile stimulation was a large suppression of oscillatory activity in the ~7-40 Hz frequency range, evident throughout most of the cortex. This suppression was maximal over the contralateral somatosensory cortex, peaking at ~20 Hz. Beta suppression at somatosensory areas peaked within ~250 ms and lasted until ~400 ms of stimulus onset, as evident in figure 18. Interestingly, over time there is a shift towards suppression of lower frequencies, a finding earlier reported following visual stimuli [75] (though no such link is suggested in [59]). As we shall see later in section 5.1, the frequency of the intrinsic neural rhythm in SII is

Figure 18: Time-frequency power changes over somatosensory channels, after unattended (top) and attended (bottom) stimulation. Adapted from [59].
suggestively slightly lower than that of SI (7-9 Hz vs. 10-13 Hz) [7,8]. Considering the ~50 ms latency of SII following SI activation [174], this may serve to explain the observed shift towards suppression of lower frequencies. This explanation is surely incomplete, and is not suggested in [59].

Beta suppression was followed by a power increase (‘beta rebound’) peaking within ~600 ms of stimulus onset, reaching higher levels for unattended than for attended stimuli. Suppression of oscillatory activity at occipital areas was much more attention-dependent. Both alpha and beta suppression at occipital sites peaked within ~200 ms of stimulus onset for unattended and ~350 ms for attended stimuli, and was roughly twice as strong for attended stimuli (see figure 19). Considering the late onset of evoked occipital activity, the authors believe it is not attributable to direct input from early somatosensory areas. Occipital beta rebound began at ~400 ms for unattended and ~600 ms for attended stimuli, reaching a similar peak ~100 ms later in both cases. Occipital alpha activity reached baseline levels within ~500 ms and ~800 ms of stimulus onset for unattended and attended stimuli, respectively.

Importantly, an induced (not stimulus-locked) 60-95 Hz gamma band response was consistently observed in the contralateral SI cortex. It rose at a similar slope for attended and unattended stimuli, peaking within ~100 ms for unattended and ~200 ms for attended stimuli. SI stimulus-induced gamma-band activity was consistently enhanced and prolonged by spatial tactile attention. This finding is compatible with those reported by Romo et al. [9,13], regarding increased phase-locking of evoked spikes in SI to the stimulus during active discrimination (see subsection 4.2). It is unclear though why the observed attentional effects were mainly restricted to the primary somatosensory cortex, with no apparent effect on frontal activity.

A multi-taper spectral analysis method was employed in this study, trading spectral resolution for reduced variance. Thus a resolution of no more than ±10 Hz is available in the 40-180 Hz range. Earlier studies have found evidence for induced gamma band activity during cognitive tasks, not only at ~40 Hz but also in the 60-90 Hz range. In a left inferior frontal sensor, the processing of an auditory pattern deviance gave rise to an increase in ~86 Hz gamma activity within ~320 ms of stimulus onset, whereas distorted noises induced ~69 Hz gamma band activity [120]. The authors [59] conclude by suggesting that “attention generally renders the reciprocal information exchange between different parts of the neural network, such as SI and SII, more effective through the stronger oscillatory coupling”.

Figure 19: Time courses of the stimulus induced power changes over contralateral channels, at several frequency bands. Adapted from [59].
4.9. *Stochastic Resonance in the Somatosensory Cortex* – Stochastic Resonance (SR) is a counterintuitive phenomenon, in which the response of a nonlinear system to a weak input signal is enhanced by the addition of a random interference ('noise') [63, 87-99]. The response amplitude is increased by adding noise to the weak signal, up to an optimal amount of added noise, beyond which signal-detectability or information content is degraded [90]. The optimal noise level is higher for weaker signals, which is counterintuitive since noise usually worsens performance [96]. In its simplest manifestation, stochastic resonance results from the occurrence of a threshold, a weak stimulus, and noise [90]. This paradigm, referred to as 'threshold SR', applies to neuronal assemblies activated by sensory inputs and perceptual processes as well. Two lucid reviews are recommended – Moss et al. 2004 review on SR in sensory information processing [90], and Gammaitoni et al. 1998 review on SR in general [99].

At the single-neuron level, a most regular spiking activity is exhibited even in the absence of an external periodic signal, due to omnipresent internal noise. An optimal amount of noise leads to a maximally coherent input, a phenomenon called 'coherence resonance' (CR) [63, 87, 97]. Sometimes the term 'doubly stochastic coherence' is used, to underline the joint involvement of two independent noise sources – intrinsic internal noise and external noisy input [87]. While coherence resonance (CR) stems from the individual stochastic dynamics of single ion channels, stochastic resonance (SR) arises from the collective properties of globally coupled ion channel assemblies [97].

SR has been demonstrated in neural excitable media undergoing transitions between monostable and bistable states [88]. In a bistable model neuron, a weak periodic signal may effectively clock the noise-induced transitions between the two stable states, causing the output to be correlated with it [89]. The bistable neuron effectively transfers energy from the random noise to the periodic signal via SR. For higher noise levels, transitions between the two states occur more stochastically, less correlated with the incoming signal\(^6\) [89]. Moreover, when the input of a bistable model neuron consists of noise and two or more periodic signals, all periodic components are enhanced via SR, and the periodic signal at the lowest frequency is enhanced the most [98]. A frequency dependence of neural SR has also been demonstrated in an important computational study of coupled hippocampal CA3 neurons [63]. In that study, stochastic resonance was observed for 4-8 Hz and 40-120 Hz sinusoidal inputs, but not for other frequency ranges. These frequencies coincide with the theta and gamma frequency bands, suggesting that SR may serve to enhance the weak intrinsic neural oscillations of the hippocampus [63].

That the human somatosensory system exhibits SR was first experimentally demonstrated in psychophysical studies by Collins et al. In 1995. Low-level input was also found useful in enhancing somatic sensation and balance control in humans, consequently reducing postural swaying in the elderly to levels near those of younger subjects [90, 93]. By 2002, Manjarrez et al. first reported EEG evidence for SR in the human somatosensory system [91]. Subsequently the same group observed phenomena consistent with SR at the spinal and cortical stages of sensory encoding in anesthetized cats [92]. In the later case, SR was also demonstrated when the signal and noise were delivered to distinct areas of the feline hind paw, insuring their mixing first occurred only in the somatosensory regions of the central nervous system. The SR behavior was abolished in the cortical, but not in the spinal recordings, after sectioning of the dorsal columns and the ipsilateral dorsolateral funiculus, suggesting that spinal neurons in the dorsal horn may also contribute to cortical SR.

\(^6\)Speculatively, one may attribute SR to higher cognitive processes such as decision making. In a sense, random advice such as astrological forecasts may enhance weak prepossessions, which are too weak to induce a state transition on their own. Further reliance on such random advice leads to decisions made randomly, irrespective of individual prepossessions. I'm not aware of experimental evidence supporting this speculation, nor have I searched for such.
In the context of this survey, the noisy spectra of motor vehicle vibrations may lead, due to somatosensory SR, to enhanced perception of their periodic components. According to [98] we expected the lower frequency components to be better enhanced via SR. At present, it is hard to estimate how a given level of vibrational noise is reflected on the curve of somatosensory signal-to-noise ratio. Consequently, we don't know if the typical vibrational noise level of a motor vehicle is higher or lower than the optimal noise level of the somatosensory system. According to psychophysical perception studies for tactile [94] and vibrotactile [96] stimuli, the optimal noise level is typically ~2-6 dB lower in magnitude than the personal level of annoyance. Seated passengers in motor vehicles are exposed to vibrations that are at least 10 dB lower in magnitude than their annoyance level [19]. Thus we may assume, as an initial guess, that the typical vibrational noise level of a motor vehicle is lower than the optimal noise level of the somatosensory system. Further psychophysical research is likely to elucidate this matter in the near future.

Some reservations depicted by Moss et al. [90] regarding the present evidence for SR in the human brain are worth mentioning. The variety of SR observations that relate to the brain may not specifically indicate a function. In fact, none of the possible sources of neuronal noise has been incorporated in the SR theory. As the authors conclude [90]: “... there is no unambiguous demonstration that naturally occurring noise actually enhances information transmission and processing, nor is it documented that neuronal systems do optimize the noise intensity for maximum efficacy or processing”. Nevertheless, my search might have missed such progress reported later than this 2004 review.

Two additional reservations should be remarked with respect to the findings reported by Manjarrez et al. in humans [91] and cats [92]. In both studies, the mechanical test stimuli consisted of single pulses delivered at a constant frequency of 2.5 Hz. In both studies, the following definition for signal-to-noise ratio was used [91]: “SNR is defined as the ratio, at the input signal frequency (2.5 Hz), of the strength of the signal peak (its area) during pulse stimulation to the mean amplitude of the activity occurring during input noise. Both the mean amplitude and the area were calculated in the frequency interval of ±1 Hz around the input signal frequency”. This nontrivial definition eases SNR calculation but is hard to justify theoretically. What is defined as 'noise' is actually the neural activity during the delivery of noisy somatosensory stimuli, averaged in the 1.5-3.5 Hz frequency range. This neural activity is expected to be more coherent than the input noise, due to coherence resonance (see above and [63,87,97]). The spectral distribution of the noisy stimulus is only mentioned in [92], where the added noise had a power spectrum ranging from 0.1 to 60 Hz and peaking at ~20 Hz. A noisy tactile stimulus is expected to evoke a stimulus-locked response, accompanied by a broadband suppression of ongoing activity, as described in detail in the previous subsections. Such an ordered response does not suit any meaningful definition of the term 'noise'. Performing a spectral analysis of the evoked response as a function of noise intensity, as done in the visual modality [95], could indicate the optimal noise level eliciting the largest evoked response, without resorting to disputable definitions of 'noise'.

Furthermore, the authors only inspected the neural activity in the spectral vicinity of the stimulus frequency, defined in [91,92] as 'signal'. Other spectral components of the neural response are clearly modulated by the addition of the periodic stimulus, as evident in figure 1 of [91] and figure 2 of [92]. In fact, in an earlier visual SR study [95], it was remarked that 5 Hz harmonic entrainment of ~10 Hz alpha activity is more reliable than its entrainment by 10 Hz stimulus frequency. In the following section we will further discuss the modulation of somatosensory neural activity at harmonics of the stimulus frequency.
5. Vibrotactile Modulation of Neural Oscillations

In contrast to the abundant literature investigating brain response to rhythmical auditory or visual stimuli, I have only found fifteen EEG:MEG studies dealing with human brain frequency response to rhythmical vibrotactile stimuli. All five MEG articles reviewed [4-8] were published by Livio Narici's group through the years 1995-2001. The ten EEG articles reviewed [18,27,28,39,40,42,70,72,73] were published by six groups through the years 1992-2006. While Narici's group distinguished between stimulus evoked response and entrainment of ongoing oscillatory activity, all the EEG somatosensory studies I found treat pre-stimulus activity as background "biological noise". Consequently the findings reported by Narici et al. are more useful for this survey. This matter is further discussed hereunder.

5.1. MEG Recordings During Vibrotactile Stimuli – One study of high relevance for this survey is reported in a 1998 paper by Narici et al. [4]. In this study, MEG recordings were taken of nine human subjects experiencing a rhythmical stimulation in one of three modalities – somatosensory, visual or auditory. Somatosensory stimuli consisted of 0.3 ms constant-current electrical pulses delivered to the left median nerve of the wrist. The visual stimuli were 30 ms green flashes, whereas the auditory stimuli consisted of 15 ms white noise bursts delivered to the left ear with an intensity of 75 dB. A train of 15 stimuli was delivered, at rates ranging from 6 to 14 Hz in 0.5 Hz steps. Neural oscillatory activity was monitored in the 5-25 Hz frequency range over the entire cortex, before, during and after the stimuli.

The rhythmical stimulation clearly induced a 10-15% global reduction of brain activity, observed at all 5-25 Hz monitored frequencies during stimulus and post-stimulus retention period (marked 'pause' in the paper). The suppression generally persisted for at-least 10-20 seconds after the stimulus train, whereas an isolated stimulation only transiently suppressed the neural activity. At-least three stimuli were needed to elicit a clear spectral suppression. This global suppression was evident following stimulation in each of the three modalities, most significantly by the somatosensory and auditory stimuli when delivered in an eyes-closed condition. In addition, the stimulus train modulated (mainly dampened) the 7-13 Hz rhythms in the modality-specific areas during the post-stimulus retention (’pause’).

Enhanced activity at the fundamental stimuli frequencies was only observed in the modality-specific areas, and only in the somatosensory and visual modalities. Citing the authors: “If the rhythm entrainment were dominating the responses, it evidently would take some time before the neuronal population generating the spontaneous activity would reentrain into a common oscillatory mode. If the driven activity were mainly composed of evoked responses, the locking should be reproducible starting already from the first stimulus of the train, although the amplitudes of evoked responses may increase or decrease the train”. Activity in the vicinity of the somatosensory hand representation area was paced by most stimulus rates, from the very beginning of the stimulus train, thus interpreted as mostly originating from evoked responses. Neural activity at the first and second harmonics of the stimulus frequencies were also observed, most clearly following a somatosensory stimulation, as evident in figure 20.

Figure 20: Spectral maps from the most active channel at the modality-specific area, for a single subject stimulated with trains of three modalities. Adapted from [4].
Importantly, rhythms outside the modality-specific areas were also modulated by the stimulus train. In particular, the parieto-occipital ~10 Hz alpha activity, usually associated with visual processing, was also suppressed by auditory and somatosensory stimuli. This suppression is evident figure 21.

This crossmodal desynchronization is suggestively related to the increased alertness caused by the stimuli trains, considering the role of the parietal cortex in attention. As neural activity at frequencies higher than 25 Hz wasn’t probed in this study, it’s unclear whether the global reduction in alpha activity was accompanied by a global or local increase or decrease in gamma activity. Moreover, the inter-modal differences observed are probably dependent on the sensory stimulation methods used in this preliminary study. Future studies may reveal a greater responsiveness to an improved auditory stimulation. This study and its predecessors [5-6] are notably unique in their attempt to distinguish between stimulus evoked response (primarily desynchronization) and entrainment of neural oscillatory activity by the rhythmical stimuli. All EEG somatosensory studies reviewed hereunder focus on stimulus evoked responses, treating non-evoked neural activity as “biological noise”.

In a subsequent paper [7], Narici et al. described a new 'sigma' rhythm, generated in the human second somatosensory cortex (SII) [7,8]. This 7-9 Hz rhythm is distinguished from the known 10-13 Hz Rolandic mu rhythm generated in the primary somatosensory cortex (SI), and the tau rhythm of the supratemporal auditory cortex.

Vibrotactile train stimuli were delivered to the median nerve of four subjects at rates of 8-12 Hz (with one subject also receiving stimuli at 4 and 6 Hz). The response amplitude was highest for stimuli delivered at 8 or 9 Hz, which is the sigma rhythm dominant frequency. The credibility of this last finding is bound by the limited range of measurements performed in this study (see figure 22).

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Figure 21: Activity changes between post-stimulation ('pause') and pre-stimulation ('rest') periods. The histograms stand for the following stimuli, from left to right: Somatosensory with eyes closed, somatosensory with eyes open, auditory with eyes closed, auditory with eyes open and visual with eyes open. The averaged suppression over the whole cortex is evident in the top inset. Copied from [4].

Figure 22: Left – Frequencies of sigma rhythm and respective stimulus frequencies eliciting greatest evoked response. Right – Response amplitudes as a function of stimulus rate, for all five subjects. Copied from [7].
While a functional distinction between 7-10 Hz and 10-13 Hz mu activity has been also suggested by Pfurtscheller et al. [114,30], the reference to an SII ‘sigma rhythm’ seem to have not caught on by other groups. Interestingly, as SII is typically activated ~50 ms after SI, a lower frequency of SII activity might explain the temporal shift towards lower frequencies in the suppression of somatosensory neural activity, recently reported by Bauer et al. [59] (see section 4.8).

In the following subsection, we shall see further EEG evidence for a unique response in the alpha frequency band to steady-state somatosensory stimulation.

5.2. EEG Recordings During Vibrotactile Stimuli – In humans, a rhythmical vibrotactile stimulus elicits an EEG brain response called the somatosensory steady-state evoked response (SSSER) [18]. SSSERs typically include the same temporal frequency as the driving stimuli and may include higher harmonics, especially in the vicinity of the primary somatosensory cortex [18,27,28,39,40,70,72,73,i]. In contrast to the frequent use of ASSR and SSVER to explore the auditory and visual systems, SSSERs are less frequently used in analyzing the somatosensory system [27]. In fact, spectral analysis of SSSER was only reported by six independent groups, only two of which using the same term for it. I have reviewed these studies more exhaustively, due to their high relevance to this survey and my own reservations about their findings, but the following summary precedes.

SSSER is potentially as useful an analyzer for the somatosensory system as ASSR and SSVER are for the auditory and visual systems. Here are some of the important findings reported in SSSER literature:

- There are large inter-individual differences in both pre-stimulus EEG spectra and SSSER spectra [70] and spatial distribution [40]. This is expectable as similar inter-individual differences were found in the auditory [135] and visual [75] modalities.

- SSSER amplitude at the stimulus frequency significantly increases when attention is directed at the vibrotactile stimulus [40,42], an enhancement of ~30% on average and probably no more than 100% [40].

- A unilateral vibrotactile stimulus mildly reduces the coherence between the bilateral somatosensory cortices at the stimulus frequency [39]. It also enhances alpha band activity, without affecting its inter-hemispheric coherence. This inter-hemispheric alpha coherence is also suggested in other recent somatosensory studies [49,58,59] despite earlier conflicting claims [36,68].

- Hand-delivered vibrations elicit SSSERs whose amplitude at stimulus frequency is about twice larger than that for foot-delivered vibrations [28].

- Clear SSSER may be elicited even by the stimulation of a single mechano-receptive afferent, though in this case the response amplitude at stimulus frequency decreases within hundreds of milliseconds [70]. Somatosensory adaptation to steady vibrotactile stimulus was reported in a single subject [72] but was subsequently controverted in a larger sample [40]. This is in contrast to founded evidence for adaptation to steady tactile stimuli and clear adaptations in other sensory modalities [40].

First named SSER by Snyder [18], then SEP by Noss et al. [73], FFR (Frequency-Following Responses) by Kelly et al. [70], S-SEP by Tobimatsu's group [27,28,69] and SSSEP by Müller-Putz et al. [i,42] and Giabbiconi et al. [40].
Unfortunately the existing SSSER literature reviewed here is mainly interested in the evoked neural activity at the stimulus frequency and its harmonics. Ongoing neural activity is treated as background 'biological noise' that is filtered [40,70,72], subtracted [27,28] or rejected [18,39,42,73]. This obsolete approach has been abandoned in other sensory modalities (see [75] for discussion), but the products of its application to the somatosensory system [18,27,28,i] are guiding the latest SSSER studies [39,40,42].

The findings reported in the SSSER literature I found are insufficient to confidently point out how ongoing neural activity is modulated by a rhythmical vibrotactile stimulus. The spectrograms provided by Snyder [18] may reflect the enhancement of 10 Hz alpha activity, by an harmonic 40 Hz stimulus and/or by a subharmonic 3 Hz stimulus. Moreover, a 7 Hz stimulus elicited a clear reduction of activity in the 10±2 Hz band, accompanying a strong response at 7 and 14 Hz. A similar 7&14 Hz effect might be evident for a 14 Hz stimulus at the spectrogram provided by Tobimatsu et al. [27], but this could very well be an artifact of their 'noise-subtraction' method. A clear enhancement of ~10 Hz alpha activity during 21 Hz stimulus is evident in the unbiased spectrograms provided by Goto et al. [39]. No such enhancement was discerned from the biased spectrograms provided by Tobimatsu et al. at [28]. Most convincingly, delivery of 26 & 31 Hz stimuli simultaneously to both hands elicited a strong enhancement of 5 Hz activity over central sites, evident in the spectrograms provided by Müller-Putz et al. [42]. This 5 Hz component is not abolished by attending to the stimulus at either hand, in contrast to such abolishment in the auditory modality [133]. The other spectrograms were useless due to filtering [40,70,72] or de-phasing [73].

A surface plot of the EEG response frequencies as a function of stimulus frequency is an instructive tool previously employed both in the auditory [50] and visual [74] modalities. In the somatosensory system, only Narici et al. [4-6] produced MEG variants of this plot (see figure 20 above).

All in all, there is clearly much room for further insightful SSSER research.

5.2.1. Snyder 1992 – Abraham Snyder [18] measured the SSSERs of 17 adult subjects experiencing hand-delivered vibrations in the 2-40 Hz range. The stimulation consisted of a sinusoidal vibration at 128 Hz whose amplitude was modulated at one of eight frequencies (2, 3, 5, 7, 11, 17, 26 and 40 Hz). SSSER spectrograms were only shown for a single subject (see figure 23 left). The spontaneous pre-stimulus activity was regarded as 'background EEG noise', whose spectrum reveals a clear 10±1 Hz alpha activity peak. The author expected a response to the stimuli at the stimulation frequency and its harmonics, treating activity at other frequencies as background noise. Accordingly he didn't discuss the modulation of 10 Hz alpha activity by the stimuli, which is clearly evident in figure 23-B:
10 Hz activity was maximal for the 11 Hz stimulation, but was also enhanced by the 40 Hz and 3 Hz stimuli, i.e. by its harmonic and subharmonic. The first and second harmonics of the 3 Hz stimulation (i.e. 6 and 9 Hz) were higher in amplitude than the fundamental 3 Hz response. Most interestingly, the 7 Hz stimulus elicited a clear reduction of activity in the 10±2 Hz band, accompanying the strong response at 7 and 14 Hz. Of all these findings, the author only noted that “background interference was pronounced in responses to 11 Hz stimuli but only minimal for 40 Hz stimuli”. Grand-averaged SSSER amplitudes and signal to 'noise' curves were computed, summing the response power over the stimulation frequency and its harmonics (figure 23 right).

SSSER amplitude was highest for 3 Hz vibrations, monotonically decreasing for higher stimulation frequencies. However this result is somewhat misleading, as the response to the 3 Hz stimulation was mostly expressed by its 6 and 9 Hz harmonics. In this sense, a surface plot of the response frequency as a function of stimulation frequency would have been more instructive. The author suggested that the peak in the signal to noise ratio at 26 Hz corresponds to “some resonance-like phenomenon”. He remarked: “The sequence: 10-18 Hz < 26 Hz < 40 Hz places the somatosensory system between the visual and auditory systems in regards to the stimulus frequency producing the most robust steady-state evoked potentials.”

Figure 23: Left – Time (A) and frequency (B) domain representations of SSSERs of a single subject. Spectrogram of spontaneous EEG activity is provided on top (D). Right – Grand-averaged evoked and spontaneous activities at stimulus frequency and its harmonics (top), and the respective signal to 'noise' curve produced (bottom). Upper trace corresponds to evoked activity and lower trace to spontaneous (unstimulated) activity. Scanned from [18].
5.2.2. Noss et al. 1996 – Noss et al. [73] performed a similar experiment, delivering rhythmical stimuli to their own median nerves at four frequencies in the 7-41 Hz range. As the spectrogram of the SSSER is only shown for 25.6 Hz stimuli, it is impossible to discern possible effects on alpha band activity. The authors once more ignored the possible modulation of alpha band activity, asserting that: “The power of the steady-state method is primarily due to the narrow bandwidth of the signal, which allows most of the noise to be easily rejected and hence avoids the necessity of prolonged averaging. For a sinusoidal input into a linear system, only the activity of the system at the stimulation frequency is of interest. For a nonlinear biological system, responses at higher harmonics must also be considered. The rest of the response is irrelevant. It is this elimination of most of the biological noise which enhances the discriminability of the signal”. While this convenient rule of thumb may be valid for some nonlinear devices (such as some mixers), it is certainly not applicable to any unknown nonlinear system. Later studies controvert its application to sensory systems, most lucidly in [75] and [136]. Unfortunately this notion gradually passes on to more recent SSSER literature with no opposing views.

5.2.3. Tobimatsu et al. 1999 – Tobimatsu et al. [27] nearly replicated Snyder's experiment (and discussion), using a similar vibrator to deliver 5-30 Hz vibrations to the hands of ten subjects. Fixed intensity (50 mN) vibrations were delivered at 9 frequencies (5, 7, 11, 14, 15, 17, 21, 25, and 30 Hz), with the 21 Hz vibrations also delivered at seven other intensities in the 1-100 mN range. Citing from [27]: “A good separation of the signal from noise was observed at high stimulus frequencies despite the relatively modest evoked potential amplitude. In particular, background interference was pronounced in response to 14 Hz stimuli but was only minimal for 30 Hz stimuli. Moreover, all but the response to 30 Hz stimuli showed predominant responses at 1F and 2F [stimulation frequency and its first harmonic, LG]”. The spectrogram of the the SSSER is harder to analyze from this paper, as the responses without vibratory stimulation were subtracted from those of the vibratory stimuli, in order “to increase the signal to noise ratio”. Once again, it was only shown for a single subject (figure 24).

This time, I see no evidence for a reduction of ~10 Hz alpha band activity during the 7 Hz stimuli, as found above in figure 23. It is evident however for the 14 Hz stimuli – apparently the ~10 Hz alpha band activity has shifted to the subharmonic 7 Hz peak. This is what the authors denote as pronounced background interference in response to 14 Hz stimuli. The same effect is possibly evident for 15, 17 and 21 Hz stimuli – The frequency of the highest peak is lower than that for 7 or 11 Hz stimuli, suggesting a ‘drift’ of the alpha rhythm towards the first subharmonic frequency of the stimuli. All these findings may be artifacts of the above-mentioned subtraction of pre-stimulus EEG spectrum.

The authors found an SNR peak at 21 Hz, versus Snyder's 26 Hz [18]. This 21 Hz response may be associated with beta band phase locking in response to tactile stimuli [49] (see section 4.6 above). The mean response amplitudes at the stimulation frequency have increased linearly with stimulus intensity, reaching a plateau at an intensity of 0.05 N.
5.2.4. **Tobimatsu et al. 2000** – In a subsequent study [28], Tobimatsu et al. probed the response of eight subjects to 17-30 Hz vibrations delivered to the palm of their right hand or the sole of their right leg. Once again, the responses without any vibratory stimulation were subtracted from those of the vibratory stimuli, in order “to increase the S/N ratio”. I have failed to locate any possible modulation of spontaneous activity in the subtracted SSSER spectra, shown again for a single subject (fig. 25).

The amplitudes of the palm SSSERs were twice as large as those of the sole SSSERs. The response amplitude at the palm stimulation frequency was greatest at 21 Hz for 6 of 8 subjects, with 19 Hz and 25 Hz for the two others. In contrast, the response amplitude at the sole stimulation frequency expressed larger inter-individual differences – three subjects had a peak at 21 Hz, two at 23 Hz, two at 25 Hz and one at 19 Hz. This is the only study I have found analyzing SSSER for any body part else than the hand.

5.2.5. **Goto et al. 2003** – In a subsequent study [39], Goto et al. probed the inter-hemispheric coherence in ten subjects experiencing 21 Hz vibratory stimulation at either hand. The 21 Hz stimulus was titled “optimal stimulus conditions”. The coherence function was calculated as the cross-correlation between the EEG signals recorded at electrodes positioned 2 cm posterior to C3 and C4 sites. Though the authors still view alpha activities as background contamination, they have shown both the unstimulated and the SSSER spectra at four electrodes in the vicinity of C3 and C4 sites. The authors were interested in the 21 Hz peak most clearly evident at the electrode posterior to C4 site. They do not mention the clear increase in alpha activity at all four electrode sites during left palm stimulation, evident in figure 26.

Coherence analysis revealed that the inter-hemispheric coherence at 21 Hz reduced from ~0.65 to ~0.55 during stimulus conditions. Coherence at other frequencies was not significantly different. Note higher ~0.7 coherence values at the alpha band, evident in figure 27.

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**Figure 25:** SSSER spectrograms for palm (left) and sole(right) stimulation. Copied from [28].

**Figure 26:** EEG spectrograms at several electrode sites for unstimulated (left) and 21 Hz stimulated (right) left palm. Adapted from [39].
The authors interpreted these findings as an inter-hemispheric desynchronization of the bilateral somatosensory areas, resulting from the unilateral stimulus. They have not reported the increase in alpha band activity while preserving its pre-stimulus coherence, which might indicate a global increase in attention. Very similar coherence values in the alpha (0.73) and beta (0.68) bands have been reported earlier [176], measured by both EEG and MEG. Such inter-hemispheric alpha coherence is also suggested in other recent somatosensory studies [49,58,59] despite earlier conflicting claims [36,68].

5.2.6. Kelly et al. 1997, 1999 – Kelly et al. [70] delivered periodic microstimulation to a single mechano-receptive afferent in the median nerve of the corresponding author. Dense multichannel EEG recordings were taken in the vicinity of the primary somatosensory cortex. The authors remark that the stimulus frequency “was initially set at 28 Hz, but in later sessions was changed to 33 Hz to escape residual background EEG activity in the 28-32 Hz range”. To their surprise, the single afferent stimuli evoked sizable EEG driving responses at the 33 Hz stimulus frequency and its spectral vicinity. These responses were “at least as large as those previously produced in the same subject by a 24-Hz, 50-μm vibrotactile stimulus delivered to the tip of a digit”, though this later stimulus has activated at least 200 mechano-receptive afferents. The driving response amplitude has systematically declined both across and within trials, interpreted as vibrotactile adaptation at timescales as short as hundreds of milliseconds.

In a subsequent study [72], similar EEG recordings were taken of the same subject, while sinusoidal vibrotactile stimuli at 27 Hz or 33 Hz were delivered to selected sites of his right hand. No consistent change in response amplitude or topography across time was observed when the stimuli was delivered to the wrist. However, reproducible temporal changes in response amplitude and topography were observed when the stimuli was delivered to any part of any hand digit. Within a few seconds, the response converged to a similar pattern to that observed earlier [70] for the stimulation of single mechano-receptive afferent. The authors suggested that this change reflects a progressive concentration of the entrained neural response, to a subset of neurons more specifically associated

![Interhemispheric coherence between pC3 and pC4 electrode sites, during stimulation of the right (left) and left (right) palm. Alpha band coherence is preserved despite the increase its amplitude (fig. 26). Copied from [39].](image-url)
with each particular locus of stimulation. The authors stress that they “do not mean to suggest that
the entire pattern of activity itself moves wholesale from one discrete SI cortical territory to another”.
Instead they suggest that “the apparent migration suggested by our EEG topographies reflects a
progressive redistribution, within the large SI region initially responsive to the stimulus, of the
sources of the entrained and synchronous activity that we detect and measure at the scalp”. The
recurrent evidence for vibrotactile adaptation deserves special attention, which it received in a
subsequent study by Giabbiconi et al. [40] (see following).

Changes in alpha band activity cannot be extracted from the SSSER measurements in these studies,
as the EEG signal was passband filtered at 27-56 Hz.

5.2.7. Giabbiconi et al. 2004 – Giabbiconi et al. [40] investigated the influence of spatial attention on the
SSSERs elicited when vibrotactile stimuli of different frequencies is applied simultaneously to both
hands. Eleven adult subjects simultaneously experienced 20 Hz vibrations at their left index finger,
and 26 Hz vibrations at their right index finger. Subjects were instructed to maintain visual fixation
on a fixation point in front of them and to detect and respond to a short decrease in stimulation
intensity in the to-be-attended vibrotactile stimulus by pressing a button with their foot. White noise
was presented in order to mask possible sounds produced by the operation of the vibrators. Only the
frequency components of the SSSERs from 18 to 22 Hz and from 24 to 28 Hz were extracted, thus
changes in alpha band activity cannot be extracted. Accordingly, the extracted SSSER waveforms
were “generally sinusoidal with fundamental frequencies at the driving vibration rate”. This reported
finding could easily be the result of the heavy filtering employed, especially if a low order filter was
used (filter order not reported). The authors also remarked that the SSSER “exhibited large
interindividual differences in the phase at different scalp sites, and therefore the grand average wave-
forms in the time domain were not informative and are not shown”. Importantly, attending to one or
the other stimulus resulted in a significant increase of SSSER amplitude at fronto-central electrode
locations contralateral to the stimulated hand – 27.7 ± 11 % and 30.6 ± 11.2 % increase when
attending the right and left fingers, respectively. Large inter-individual differences were found for
this figure, with greatest enhancement of 95.5 % found for attending the right 26 Hz stimulus. Citing
from [40]: “This increase could not be attributed to phase synchronization, as no significant
difference in the Fourier components between attended and ignored steady-state stimulation was
observed [...] [This amplitude increase] suggests an enhancement of neural responses to spatially
discrete flutter vibration when being attended. Similar amplitude modulations of steady-state visual
evoked potentials have been interpreted as evidence of an early sensory gain control mechanism that
enhances the signal-to-noise ratio of the sensory input within the 'spotlight' of spatial attention and
facilitates their transmission to higher cortical areas for further preferential processing. This
interpretation is further supported by the fact that we found no consistent phase shift between
attended and unattended vibration”. These results agree with previous findings in monkeys [9,10,13]
and humans [38,174,177] regarding the increased activity of SI and especially SII cortices when a
vibrotactile stimulus is being attended.

In contrast to the fast adaptation to vibrotactile stimuli reported by Kelly et al. [70,72], Giabbiconi et
al. found no differences in SSSER amplitude between the early and late time window of stimulation
for any frequency in all experimental conditions. The authors refer to three earlier animal and human
studies, all have shown that adaptation to flutter vibration does not occur within short time periods of
a few seconds.

5.2.8. Müller-Putz et al. 2006 – Last but not least, Müller-Putz et al. [42] attempted to utilize the effects
of spatial attention on SSSER for the development of a brain-computer interface. In a protocol
similar to Giabbiconi et al.’s [40], vibrotactile stimuli of different frequencies were applied
simultaneously to the index fingers of five subjects. Prior to the main study, a procedure termed
'frequency screening' was employed to determine the stimulus frequency which elicits the largest increase in EEG power, at the spectral vicinity of the stimulus frequency. In this procedure, elaborated in an earlier unreached paper [i], the 17-35 Hz frequency range was probed in 2 Hz steps. The so-called 'resonance-like frequencies' identified for the five subjects were 25, 25, 27, 31 and 31 Hz. Vibrotactile stimuli at that frequency was delivered to the right index finger, and a similar stimuli at 5 Hz less was delivered to the left index finger. As proposed by Giabbiconi et al. [40], a short decrease in stimulus amplitude (‘twitch’) marked the to-be-attended finger, and acoustic noise was used to mask the stimulator noise. Both online and offline classification algorithms were applied, in attempt to determine which finger was attended based on changes in the EEG power spectrum.

The offline classification algorithm reached an accuracy of more than 80% in two of five subjects. Worse results were obtained for two others, suggestively due to concentration problems, while a fifth subject dropped out. EEG spectra are only shown for one of the two 'successful' subjects, who was acquainted with the system:

![Figure 28: SSSER spectrograms for a single subject attending the right 31 Hz (top) or the left 26 Hz (bottom) hand. Note 5 Hz component at the three electrode sites. Copied from [42].](image)

Switching attention from the right (31 Hz) to the left (26 Hz) stimuli clearly suppressed the ~31 Hz component over the C3 electrode while enhancing the ~26 Hz component over the C4 electrode. Both ~26 Hz and ~31 Hz peaks are evident in the power spectra over the Cz electrode, and their relative dominance is clearly modulated by attention. These findings are in accordance with the attentional effects reported earlier by Giabbiconi et al. [40], though they're not quantified in this study [42].

Most interestingly, a strong ~5 Hz component is evident at all three electrode sites, at both attentional modes (right and left). It is strongest over the Cz electrode site, followed by the C3 electrode site (subject handedness was not reported). Such a strong 5 Hz activity, on top of the ~1/f power distribution, is clearly related to the vibrotactile stimuli, as it overshadows the normally predominant ~10 Hz alpha activity [53,76,124]. Regrettably, pre-stimulus EEG spectra at these electrode sites are not provided, nor is the evoked EEG spectra before the attentional cue was provided. Therefore we cannot quantify the 5 Hz enhancement or identify the possible modulation of pre-stimulus alpha activity.
It should be emphasized that the subjects in this experiment were instructed to attend only one stimulated finger at each trial, counting the number of 'twitches' in its amplitude. They were not asked to attend both stimuli simultaneously or to discriminate their frequencies. As we saw earlier in section 4.2, in a frequency discrimination task conducted with monkeys, the neural population response gradually became dominated by responses that were a function of the frequency difference (f2-f1). Furthermore, as we saw earlier in section 2.5, in the auditory modality, attending to one ear at a time abolished the binaural beat ASSR [133]. Thus, the appearance of a strong ~5 Hz component in figure 28 is certainly nontrivial. It is somewhat surprising the dignified authors of [42] did not attend to this finding. Then again, when one looks for “sinusoidal signals” which are “superimposed by random noise” [42], it is possible to overlook other effects.
6. Cross-Modal Modulation of Neural Activity by Vibrotactile Stimuli

6.1. Audiotactile Interactions – Caetano & Jousmäki [17] found clear evidence for the activation of human auditory cortical areas by vibrotactile stimulation alone. 200 Hz vibrations were delivered to the right hand fingertips of 11 adults undergoing MEG recordings, while using earplugs. All subjects reported a weak percept of vibration and a perception of a sound, only while touching the vibrating device (a tube). In a subsequent control experiment, the same procedure was performed with a patient whose right median nerve was cut in an injury, losing sensation in three fingers. That patient only reported perception of a sound when touching the vibrating tube with his healthy fingers (see [17] for further control considerations).

In all subjects, first responses to the vibrotactile stimuli originated in the primary somatosensory cortex (SI), followed by activations in the auditory cortices and secondary somatosensory cortex (SII). The SI response peaked within 60 ms of stimulation onset, whereas auditory and SII activations consisted of transient responses at 100-200 ms, with additional auditory sustained activation in most subjects at 200-700 ms. Specifically, no significant difference was found between the locations of the dipole sources in the auditory cortices, measured by MEG during auditory stimuli and vibrotactile stimuli. No spectral analysis was reported in this study.

According to the authors, these results agree with previous studies in both monkeys and humans, that indicate multisensory convergence at early stages of auditory cortical processing. Audiotactile interactions are bidirectional – the perception of a surface texture and roughness can be modified by manipulating the frequency content of the sounds produced by touching it\(^8\). The underlying mechanisms for multisensory interactions are not well understood yet [17].

In the context of this survey, audiotactile interactions may be the “long sure path” for vibrotactile modulation of synchronous neural oscillations, via audiotactile excitation of an ASSR. For instance, a rhythmic 40 Hz vibration should elicit a 40 Hz ASSR, which in turn might be reflected in cognitive performance. Hypothetically, such a crossmodal modulation of oscillatory activity should be observable even if the ongoing oscillatory activity in the somatosensory system is in itself insensitive to rhythmic stimuli. Therefore, one should be careful not to immediately attribute any cognitive effect of vibrotactile stimuli to the somatosensory system alone.

6.2. Visuotactile Interactions – To be added based on literature provided by Burton et al. [198].

\(^8\)For elaboration see Guest et al., 2002 http://dx.doi.org/10.1007/s00221-002-1164-z
7. Human Whole Body Vibrations in Motor Vehicles

7.1. Summary – Human adults exposed to vertical whole-body vibrations have a major power absorption peak at about 5 Hz (half-max width ~3-7.5 Hz). Human infants have a single power absorption peak at about 7.4 Hz (half-max width ~5-11 Hz), which is smoother and broader than the absorption peak in adults (see figure 30). Infants absorb vibrational energy per unit mass almost as efficiently as adults.

The most prominent contribution to the spectra of the seat vibrations in idle running conditions (engine on, car at rest) comes from the second order of the motor engine frequency. In moving vehicles, vehicle-road interaction contribute a dominant peak at around 13 Hz. The residual normalized absorbed power at ~13 Hz is higher for children than for adults (see figure 30), which yields a higher dose of vibrational energy per unit mass absorbed by children in moving vehicles. However, comparative research between adults in children is still in its early stages.

7.2. Introduction – The effects of whole-body vibrations on perception and comfort is often associated with vibrations in the 1-100 Hz frequency range. Vibrations at higher frequencies are mostly perceived as audible cues, as the sensitivity of the human ear increases whereas the sensitivity of human body decreases [19]. The resonance frequencies of the seated human body are sketched in figure 29.

One of the standard methods to evaluate human exposure to vibrations is to calculate the power absorbed by the body during such vibrations [20-1,24]. Let \( F(f) \) be the instantaneous oscillatory force applied on a body with frequency \( f \). Let \( v(f) \) be the instantaneous velocity of the body. The instantaneous power \( P(f) \) is their scalar product:

\[
P(f) = F(f) \cdot v(f) = |F(f)||v(f)|\cos(\theta_{F,v})
\]

Where \( \theta_{F,v} \) is the phase between the force applied on the body and its velocity.

The absorbed power can be determined from the cross spectrum between the force and velocity:

\[
P_{abs}(f) = |G_{Fv}|\cos(\theta(f))
\]

Where \( |G_{Fv}| \) is the modulus and \( \theta(f) \) is the phase of the cross-spectrum between the driving force and the outcoming velocity. In spectral density form the absorbed power is expressed in units of \( [N \text{ m s}^{-1} \text{ Hz}^{-1}] = [\text{Joule}] \). Integrating the absorbed power over the frequency domain yields the total power absorbed by the body, in watts. This measure is sensitive to both subject weight and acceleration magnitude at any frequency, which is susceptible to minor experimental deviations. Since absorbed power increases in proportion to the square of the acceleration, Mansfield and Griffin [20] have suggested the following normalized measure:

![Figure 29: Resonance frequencies of the seated human body. Copied from (19).](image)
Normalized-\(P_{\text{abs}}(f) = \frac{P_{\text{abs}}(f)}{|G_a(f)|}\)

where \(G_a(f)\) is the power spectrum of the acceleration.

The normalized absorbed power can be used as a weighting function, indicating the frequencies in which a given body is more sensitive to applied vibrations. It takes units of \([\text{N s}^3 \text{m}^{-1}] = [\text{Kg second}]\). Integrating it over the frequency domain yields the total normalized absorbed power [20], in units of mass [Kg].

Since the absorbed power is also linearly proportional to body mass, Mansfield et al. [21] and Giacomin [24] have suggested the following double-normalized measure:

Double-normalized-\(P_{\text{abs}}(f) = \frac{P_{\text{abs}}(f)}{m|G_a(f)|}\)

where \(m\) is the body mass and \(G_a(f)\) is the power spectrum of the acceleration. The double normalized absorbed power takes units of \([\text{N s}^3 \text{Kg}^{-1} \text{m}^{-1}] = [\text{second}]\), that can be integrated over the frequency domain to obtain a dimensionless double normalized total absorbed power.

7.3. Absorbed Power in Humans – The normalized absorbed power of a point mass or an ideal rigid body is zero, independent of frequency. However, the normalized absorbed power of the seated human body is highly dependent on frequency. The dominant contribution to the power absorbed by humans seated in motor vehicles comes from vertical whole-body vibrations [22-3,25]. Figure 30 presents the normalized and double-normalized power absorbed by human males, females and small children, during vertical whole-body vibrations.

As observed in figure 30, the normalized absorbed power spectra of human adults exhibit a peak occurring at about 5 Hz. A second peak (shoulder), about four times lower in magnitude, is centered at about 10 Hz. The differences in the resonance frequency and magnitude between males and females are not significant [21]. The half-max spectral width of the peak is about 3-7.5 Hz. The peak in the normalized absorbed power is dependent on the magnitude of the vibration: the peak is greater in magnitude, and lower in frequency, with greater magnitudes of vibration [20,21]. For instance, a tenfold increase in vibration magnitude, from 0.25 ms\(^{-2}\) to 2.5 ms\(^{-2}\), lead to a 38% increase in the peak normalized absorbed power, and a 23% reduction in the mean frequency of the peak – from 5.86 Hz to 4.49 Hz [20]. As the r.m.s. vibration magnitudes of the seat base on a bumpy road do not exceed 1 ms\(^{-2}\) [22], this weak nonlinear phenomenon can be neglected for the purpose of this work.

![Figure 30](image.png)

*Figure 30: Normalized and double-normalized absorbed power spectrograms of adults and children. Adapted from [24].
The absorbed power spectra of small children shown above was calculated by Giacomin [24] based on a sample of eight children whose ages ranged from 3 to 23 months. The mean frequency of peak power absorption was found to be approximately 7.4 Hz for the small children as opposed to 4-6 Hz for adults. The half-max spectral width of the peak is about 5-11 Hz. Seven of the eight children were characterized by absorbed power curves which contained only a single resonance peak. Only the largest child (a 85.0 cm tall, 23 months old female, weighing 12.4 kg) exhibited a dynamic response which might suggest two whole-body resonances, as found for seated human adults. Compared with adult power absorption data from [20], the total normalized power absorption for the children was approximately 12% that of adults. In double normalized form, the total double-normalized absorbed power was 0.0016 for children, compared with 0.0018 for adults (in dimensionless units, see above introduction). Mean child absorption was thus approximately determined as 86% that of adults, with methodological differences between measurements in [20] and [24] limiting the accuracy of this result.

7.4. Motor Vehicles Vibrational Spectra – The spectra of the seat vibrations in idle running conditions (engine on, car at rest) exhibit a typical peak-trough structure, which can be interpreted in terms of harmonics of motor engine frequency [19]. Figure 31 presents the averaged spectra for seat vibrations, with an engine running in 800 rpm (13.3 Hz).

As evident from these graphs, the most prominent contribution comes from the second order of the motor engine frequency – about 27 Hz in this case. This prominent 2nd order contribution is present in vehicles with 4-cylinder engines [19]. Higher harmonics dominate the higher frequency region. The same resonances are found in all three directions - fore-aft, lateral and vertical.

![Figure 31: Averaged spectrograms for seat vibrations of petrol- (left) and diesel- (right) engine car. Represented car classes are upper middle class (top), middle class (middle) and small class (bottom). Copied from [19].](image-url)
In traveling vehicles there are more significant vibrations at frequencies lower than 20 Hz, possibly introduced by the suspension system. Figure 32 presents the acceleration spectral power density functions measured at the seat of a Ford Mondeo traveling on a street road at 64 km/h (40 mph).

![Figure 32: Acceleration power spectral density functions measured for a car traveling at 64 km/h on a street road. Measurements were taken at the four corners of the seat base and at its backrest. Note different scales for the different vibration directions, with the most significant vibrations in the vertical direction (right column). Copied from [22].](image)

The spectral distribution is more dispersed in a traveling vehicle than in idle running conditions (compare figures 31 and 32). A ~13 Hz peak is observed in the spectrograms of vertical vibrations, which is absent from the idle running vehicle vibratory spectrogram in figure 31. Thus this peak may be attributed to vehicle-road interactions, possibly a resonance of the vehicle's suspension system. A similar peak is observed in the spectrogram of another traveling vehicle (figure 33), as discussed below.

I have found only one preliminary study [23] calculating the acceleration power spectral density at the interface between a child and his seat in a traveling vehicle. In this study, a 7 months old male occupied a child seat placed on the front passenger seat, and a 28 months old female occupied a child seat placed in the middle of the rear passenger seat. Measurements were taken in a car (a Rover 214) driving over a paved surface at 40 km/h. The acceleration power spectral densities at the interface between the children and their child seats is presented in figure 33, alongside with a similar measurement for the driver.
At the driver's body resonance, around 4 Hz, she absorbs more energy than the children. At the children's body resonance, around 7 Hz, both children absorb more energy than the driver. At higher frequencies, the child in the front seat absorbs more energy than the driver, possibly since present child seats are optimized for safety and not for vibrational comfort [23]. The peak at ~13 Hz is derived from the main peak of the power spectral density of the seat acceleration (shown in figure 6 of [23]). As mentioned above, a similar peak is present in the traveling vehicle vibratory spectrogram (figure 32), suggesting that it may be attributed to vehicle-road interactions. Whatever is its source, this peak is closer to the body resonance of children, than to the body resonance of adults. Accordingly the residual normalized absorbed power at ~13 Hz is higher for children than for adults (see figure 30). Thus, in moving vehicles, children are expected to absorb a higher dose of vibrational energy per unit mass than adults. Comparative research however is still at its early stages.
8. Neural & Cognitive Effects of Whole Body Vibrations on Adult Humans

In this section we shall review the cognitive effects of whole body vibrations on adult humans, as reported in the literature. Its effects on human infants are discussed in section 9, due to notable methodological differences between the two kinds of studies. Throughout this section, vertical whole body vibrations will be called WBV.

8.1. Debated Effects of Whole Body Vibrations on Cognitive Performance – Ljungberg et al. [100] used the Sternberg paradigm to examine the effects of whole-body vibrations and noise on cognitive performance. 54 subjects were divided into three groups, exposed to three levels of noise and WBV. The vibratory stimuli consisted of sinusoidal 16 Hz vertical WBV at r.m.s. magnitudes of 1.0, 1.6 and 2.5 ms^-2. The acoustic stimuli consisted of helicopter sound, dominant at 21 Hz, at intensity levels of 77, 81 and 86 dB(A). The subjects performed the Sternberg task while being randomly exposed to noise, WBV, both stimuli combined or no stimuli.

No significant differences in performance were found between the different environmental exposures, neither in terms of mean reaction time nor in response accuracy. The subjects consistently rated the difficulty and of the memory task as higher while exposed to the combined stimuli, giving it higher annoyance ratings. Those exposed to the highest intensity levels of noise and WBV also found the situation significantly more annoying, despite performing equally as well in the Sternberg task.

It should be noted that the lowest vibration magnitude used in this study (1 ms^-2) is higher than that experienced in cars, even over bumpy roads [22], as elaborated in the previous section. The vibrational stimuli in this study [100] were designed to match those in a 1990 unreached study by Sherwood and Griffin [iii]. In that study [iii], sixteen subjects performed the Sternberg task while exposed to sinusoidal 16 Hz WBV at the same magnitudes as in [100]. Mean reaction time was significantly higher during all vibrational conditions, but response errors only rose significantly during the 1.0 ms^-2 condition. These results are definitely inconsistent with those later reported by Ljungberg et al. [100], whose sample size was much larger.

In a subsequent 1992 unreached study by Sherwood and Griffin[jv], twenty subjects performed a simple associative learning task, while exposed to strong (2 ms^-2 r.m.s.) sinusoidal 16 Hz WBV. Reportedly, the vibrated subjects exhibited significantly impaired the rates of learning, with respect to those of twenty non-vibrated subjects in the control group. Memory recall processes, tested in another session one week later, were unaffected by the recall environment, arguing against context-dependent effects. It is unclear why the same subjects weren't asked to carry out the learning task under both vibration and no-vibration conditions, thereby reducing the effects of inter-individual variability. Then again, this may have been clarified in the article body.

Last but not least, Setia Hermawati [101] investigated the effects of noise and random whole-body vibrations on the performance of twelve subjects at the Sternberg task. Pink noise was used in two levels – 56 dBA (control) and 85 dBA. The vibratory stimuli consisted of 2-10 Hz Gaussian random vibrations, at r.m.s. acceleration magnitude of 0.15 ms^-2, weighted according to ISO 2631 for equal sensation at each frequency. Whole body vibrations were delivered at either one or both of two directions – vertical and fore-aft. Thus eight experimental conditions were used in this study – low or high level noise, with or without vibrations at either or both vertical and fore-aft directions.

No effect of noise and vibration on performance in the Sternberg task were demonstrated. Accuracy and mean reaction time were similar with and without the vibratory stimuli. The only significant results were higher levels of annoyance, frustration and effort reported following the high level
noise. Dividing the subjects into high and low sensitivity groups according to their reported annoyance and effort, revealed a mildly significant (p<0.1) effect on reaction time to negative probes only. The reaction time of the low sensitivity group for negative probes was ~7% lower than that of the high sensitivity group.

All in all, studies on the effects of whole body vibration on cognitive performance have tended to produce conflicting results. Two of four studies [100,101,iii,iv], with smaller sample sizes (16 and 20 vs. 54 and 12), find detrimental cognitive effects for vertical whole-body vibrations, whose magnitude is stronger than experienced in modern cars. Mixed results are also reported regarding other neural and physiological effects of whole body vibrations, as we shall see in the following subsections.

8.2. Effects of Whole Body Vibrations on Driving Fatigue – Jiao et al. [102] investigated the effects of whole body vibrations on driving fatigue and heart rate variability, during simulated driving. Heart rate variability is a measure of the relative power of three periodic components in cardiac activity [167]: 0.04-0.08 Low frequency, ~0.1 Hz middle frequency and 0.15-0.5 Hz high frequency. The high frequency component is widely used as a marker of parasympathetic activity [102,167]. The low frequency component is influenced by both the sympathetic and parasympathetic nervous systems [167], thus its use in the present study [102] as a marker of sympathetic activity is more disputable.

Sixty subjects participated in a simulated driving for 90 minutes, while exposed to 1.8 Hz, 6 Hz or no WBV, at a realistic magnitude of 0.5 m/s². Fatigue symptoms were more frequently reported during WBV conditions. This correlation was statistically significant for the 6 Hz WBV, for the following sayings, with descending statistical significance: 'want to lie down' (p<0.003), 'stiffness of shoulder' (p<0.005), 'easily absent-minded' (p<0.007) and 'physically tired' (p<0.011).

The physiological expression of this increased fatigue via heart rate variability was statistically significant to a lesser extent (p<0.05). During the experimental period, the high frequency component was significantly higher for either WBV group with respect to the no-WBV group, but the low frequency component was only significantly lower for the 6 Hz group. This was taken by the authors as an indication that the 6 Hz WBV influenced both sympathetic and parasympathetic nervous activities, while the 1.8 Hz WBV mainly influenced parasympathetic nervous systems.

It should be noted that motion sickness is associated with a decrease in parasympathetic activity and an increase in sympathetic activity [167], which is quite the opposite effect than reported in this study. In subsection 8.6 we shall review further experimental evidence from onboard EEG recordings of motor vehicle drivers. Unfortunately, existing measurements cannot be used to detect the effects of whole body vibrations on driving fatigue, for reasons that will be addressed. More useful experimental evidence is reviewed first, in the following subsections.

8.3. Effects of Whole Body Vibrations on Neuronal Activity – Maikala et al. [107] evaluated the effects of whole-body vibrations on regional cerebral oxygenation and blood volume in thirteen subjects, using near-infrared spectroscopy. Only a single prefrontal area was probed in this study. Strong (r.m.s. ~9 ms⁻¹) vertical WBV were delivered at one of three frequencies – 3, 4.5 and 6 Hz, either with or without backrest support. During the fifth minute of each 8-minutes WBV exposure session, the subjects performed rhythmical hand grip contractions at 0.2 Hz. This task was used to simulate the operation of manual controls by drivers and pilots, though the magnitude of WBV applied in this study was more than 10 dB stronger than experienced by passengers in modern cars.
WBV elicited small increases in cerebral oxygenation and blood volume, both parameters corresponding to an increase in neuronal activity. A highest increase was found for 4.5 Hz WBV, with an insignificantly smaller increase for 6 Hz WBV, in agreement with a vibrational power absorption peak at ~5 Hz, as reported in section 7.3. During hand grip contractions, cerebral oxygenation and blood volume values were 94% and 58% higher than during WBV alone, respectively, in agreement with earlier studies of activation during motor tasks. Backrest support elicited a non-significant increase in both cerebral parameters.

These findings suggest a functional significance for the frequency dependence of the vibrational power absorption curve, qualified earlier in section 7.3. Nevertheless, it is surely too early to assert that humans are most sensitive to WBV at their own power absorption peak frequency (~5 Hz for adults, ~7-8 Hz for infants). Further studies, probing more brain regions and a broader vibrational frequency range, are clearly required to refine or refute this expected connection.

8.4. Effects of Whole Body Vibrations on Auditory Evoked Potentials

In a series of studies from 1980 to 1992, Seidel et al. investigated the effects of whole body vibrations and noise on auditory evoked potentials (AEP). In all their studies reviewed henceforth [103-105], the EEG data was treated with a subtraction technique in order to eliminate the vibration-phase-locked neural activity. This subtraction technique eliminates much of the information relevant for this survey, but some noteworthy findings remain.

In a 1986 study [103], nine subjects experienced sinusoidal WBV at one of four frequencies (1, 2, 4 and 8 Hz), and two intensities. The high intensity WBV were matched to the exposure limit for 25 minutes according to ISO 2631, and the low intensity were 16 dB lower in magnitude. The r.m.s. acceleration values of the low and high intensities were in the 0.57-1.13 ms\(^{-2}\) and 3.6-5.53 ms\(^{-2}\) ranges, respectively. The AEP N1-P2 amplitudes were systematically lower during WBV conditions, decreasing by as much as ~30 % for the high intensity 1 Hz WBV, with respect to no-WBV conditions. Moreover, electrocardiogram (ECG) recordings revealed a significant reduction in heart rate for the high intensity 1 Hz WBV. Both effects on AEP and heart rate have gradually diminished for higher WBV frequencies and lower intensities. On the face of it, these findings suggest that 1 Hz WBV are most effective in eliciting decreased arousal. However, several later studies\(^9\) suggest that the intensity curves set at ISO 2631 are inaccurate in the 1-10 Hz frequency range. Thus the obtained results may derive from excessive accelerations for the 1 Hz stimulus. Considering the relatively high acceleration magnitudes probed in this study with respect to motor vehicle vibrations (typically less than 1 ms\(^{-2}\) in r.m.s. magnitude), these results may be taken as a preliminary upper bound for their effects on AEP and heart rate.

In a 1990 study [104], nine subjects were seated in front of a large checkerboard pattern, with their field of vision confined to it. AEP were calculated in one of three conditions - no vibration, sinusoidal 0.6 Hz WBV, or sinusoidal 0.6 Hz vibration of the checkerboard pattern. Vibration acceleration r.m.s. magnitude was 1.85 ms\(^{-2}\). A similar reduction of AEP N1-P2 amplitude was observed for both vibration conditions. This finding suggests that the relative motion between a seated person and his/her visual surround is sufficient to elicit the de-arousal effects on AEP observed during WBV. If further experiments corroborate and generalize this outcome for unbiased EEG recordings, direct mechanical effects of WBV may be rejected, though vestibular and somatosensory responses may also be triggered by the vibrating visual stimuli. Such an outcome may be of experimental use, as it’s always safer to vibrate the visual field of a subject, especially in the case of infant subjects. The authors suggested that the AEP amplitudes were attenuated by a “latent kinetosis” elicited by the stimulated sensory mismatch.

In a 1992 study [105], twelve subjects were exposed to white noise at two intensity levels (60 and 80 dBA) with or without 2 Hz whole body vibrations (r.m.s. 2 ms$^{-2}$). The WBV had a significant general effect on the estimation of loudness – noise was judged as more intense during WBV conditions. This findings is congruous with a synergistic effect coming to play for the combined exposure to WBV and noise. However, the WBV had no significant effect on the AEP N1-P2 amplitudes, whereas these amplitudes were systematically lower for the higher noise levels. The authors suggested inter alia that the missing that the missing systematic effect of WBV is explained by “a moderately increased arousal due to a less monotonous situation and increased proprioceptive affereces [sic] during isolated WBV exposure”. This explanation is compatible with the findings reported in a later study [106], investigating the effects of noise and vibration on human hearing thresholds, as reviewed in the following subsection.

8.5. Effects of Hand-Arm Vibrations on Hearing Thresholds – Zhu et al. [106] exposed nineteen subjects to noise and hand-delivered vibrations, subsequently measuring their hearing threshold. The noisy stimuli consisted of 90 dBA white noise delivered to the right ear, whereas the vibratory stimuli consisted of very strong (30 ms$^{-2}$) 60 Hz vibrations delivered to the right hand. The hearing threshold was measured during a one minute pause between consecutive three minute exposures, and for five minutes after finishing a 20 minutes set of five exposures. Exposure to noise caused a temporary threshold shift of hearing (TTS), and exposure to combined vibration and noise produced significantly greater TTSs. Exposure to vibration alone produced almost no temporary threshold shift of hearing.

These findings are congruous with those reported earlier by Seidel et al. [105]: A given noise is perceived as louder when combined with intense vibrations, thereby temporarily further increasing the threshold, as found in [106]. Increased arousal may compensate for this effect, yielding comparable amplitudes for auditory evoked potentials (AEP), as found in [105]. This explanation may be tested by modifying Zhu et al.’s experimental protocol [106], adding to it AEP measurements during exposure to noise or vibration. According to this explanation, AEP N1-P2 amplitudes should be higher during exposure to vibration alone, than during no-vibration conditions, due to vibration-induced increased arousal. Anyway, the applicability of these findings to motor vehicle vibrations is debatable, as the vibrations delivered were more than 15 dB stronger than those experienced by passengers in modern motor vehicles.

8.6. Inapplicability of Onboard EEG Recordings of Drivers – Drivers' Drowsiness and inattentiveness are among the main causes of traffic accidents [111-113]. Drivers usually get drowsy within an hour of continuous driving [111], often not aware of their own waning alertness [112,113]. In recent years, several research groups try to develop on-board systems, that will monitor the driver's EEG power spectrum, issuing an early warning in case of a dangerous decrease in alertness and vigilance. Ostensibly, such an on-board system could provide direct evidence for the hypothetical modulation of neural activity by motor vehicle vibrations. Unfortunately, my non-exhaustive literature search in this direction has failed to produce useful findings, an outcome elaborated as follows. More importantly, even an exhaustive literature search for drivers' EEG power spectrum is of limited value, as any vibrational effect is probably masked by dominant effects of attention to visual stimuli, stress and fatigue. In this sense, non-involved passengers and infant passengers in particular may exhibit a behaviour which is more directly related to ongoing motor vehicle vibrations. In conclusion, an existing onboard EEG monitoring system may be of use in tracking passengers' neural response to whole body vibrations, yet existing literature regarding the development of such a system is apparently useless for this purpose.

Wu et al. [111] have taken EEG recordings of ten subjects in a virtual-reality simulator, while keeping a simulated car driving at a fixed velocity of 100 km/h on a freeway. The car was constantly...
and randomly drifted away from the cruising lane, and the driver had to compensate for the drifts by controlling the wheel. A correlation coefficient was calculated between fluctuations in driving performance and the concurrent changes in the EEG spectrum. Interestingly, a positive correlation (~0.2-0.6) was found between driving performance and EEG spectral power density in the ~5-20 Hz region, at all EEG electrode sites. A weaker negative correlation (~0-0.2) was found for higher EEG frequencies, which is rather counterintuitive considering the role of gamma activity in attention and cognitive performance. EEG signals from electrode sites Cz and Pz were adequate to continuously assess the driver's alertness level, a neural network estimator exceeding a correlation of 0.7 between the estimated and actual driving performance. As no vibratory stimuli were simulated in this study, it demonstrates the EEG power spectra during driving in a vibration-free environment. Potentially, one may use such a simulated environment to repeatedly take EEG measurements during simulated driving, with and without whole body vibrations, possibly revealing distinct effects of WBV on drivers' neural activity and performance. Specifically, such a carefully controlled environment enables to investigate the effects of a vibrating field of view, with and without whole body vibrations. Thus the similarity in effects of WBV and vibrating field of vision, reported earlier by Seidel et al. [104], may be tested with both neural and cognitive measures, using present-day technology.

Pastor Cerezuela et al. [112] have taken onboard EEG measurements of fourteen drivers, driving at 100-120 km/h over a distance of 90 km, either on a motorway or on a conventional road. Two EEG electrode sites were used – a central (C3-A2) and an occipital-parietal (O2-P4) derivations. A higher ratio between the EEG spectral power densities on the 4-12 Hz and 12-30 Hz bands was taken as indicator for lower alertness. The only possibly significant effect found \( (p=0.03) \) was a higher 'alertness level' on the motorway than on conventional road, during the 5-15 minutes time interval of driving, only in the occipital-parietal electrode site. That the difference in a single pair of histograms out of 16 pairs turns out to be mildly significant \( (p=0.03) \) may very well be a matter of chance. Thus I think it's safer to assert that this study found no significant differences in the suggested 'alertness indicator', between driving on a motorway and driving on a conventional road. It is unclear whether EEG contaminations caused by blinking and head movements were excluded from the automatic calculation of spectral power density (and if so how).

In a subsequent study, Pastor et al. [113] have taken onboard EEG measurements of fourteen drivers, driving either one of the same two stretches of road as in [112]. In this study, a single EEG electrode site was used at an occipital-parietal (O2-P4) derivation, with the EEG spectral power density at the 8-12 Hz alpha band taken as an alertness indicator. According to the authors, “the higher the alpha value, the lower the alertness level”, a debatable argument that is further discussed in section 11.1. In addition, the average number of looks at the rear-view mirror per minute was taken as a behavioural indicator of driver alertness. This time, significant correlations were found between the two parameters, over the two types of road. The frequency of rear-view mirror use was negatively correlated (-0.42) with occipital alpha band power while driving on the motorway, and positively correlated with it to the very same extent (0.42) while driving on the conventional road. Over the motorway, a higher negative correlation (-0.55) was found between the occipital alpha band power at a given minute, and the frequency of mirror gazing at the following minute. Over the conventional road, the same correlation was of a lower positive value (0.27). The authors suggest that the difference in correlations between the two road types is derived from different driving styles, as drivers over conventional roads should look ahead more often for unpredictable stimuli. A much higher baseline level of occipital alpha band power was measured over the conventional road than over the motorway, which could not be distinguished from inter-individual differences between drivers of the two groups. Letting the same drivers to drive over both road types may have clarified this point, possibly relating an increased occipital alpha activity to driving over conventional roads.
Considering the numerous behavioural differences between driving one road and another, such an
effect cannot be attributed to a single minor parameter such as the increased magnitude of WBV
experienced over conventional roads.

8.7. Long Term Effects of Whole Body Vibrations – The effects of whole body vibrations on the psycho-
emotional state of human adults has been little studied [108]. One occupational study [108]
administered the Profile of Mood States test to 137 forklift truck drivers, occupationally exposed to
intense whole-body vibrations (vibrational spectral intensity not reported) and noise (75-80 dB). 156
comparable workers not occupationally exposed to WBV served as a control group. A significant
difference in the response to the neuro-behavioural test was found for all six factors examined, most
notably for 'fatigue-inertia', 'depression-dejection' and 'tension-anxiety'. A significant (p<0.02)
correlation was found between the length of occupational exposure time and age, and the score
obtained for all factors in the exposed group.

These findings are in line with other works (such as [19,26]) which used perception-threshold tests
and questionnaires to reveal detrimental effects of motor vehicle vibrations on perception threshold
and discomfort. Still, long term effects of prolonged exposures to vibrations may derive from
pathogenic mechanisms, initiated by mechanical damage to blood vessels and nerve elements (see
[110] for review). These mechanisms have little or nothing to do with the immediate effects of
vibratory stimuli on sensory neural response, which is the issue of interest in this work. Therefore,
we first have to better understand the immediate neural and cognitive effects of WBV, before
suggesting any linkage between these and the long term detrimental effects of intense WBV.

Notably, recent studies suggest that the long term effects of intense WBV may not be detrimental
only. Brief daily exposures to intense WBV in the 15-60 Hz frequency range is considered as a
possible non-pharmacological intervention, to prevent or reverse bone loss in Osteoporosis patients
[109].
9. Modulation of Infantile Vigilance by Rhythmical Sensory Stimuli

This section covers the modulation of infantile vigilance by two kinds of stimuli – continuous stimuli and rhythmical 'rocking' stimuli. Both kinds of stimuli lead to an immediate reduction in infantile vigilance, possibly due to the same neural mechanisms. Relevant literature is surprisingly rather old, mostly dating back to the 1970s, though I might have simply missed later experimental studies. Two newer sources of clinical evidence regarding the soothing effects of rocking are then reviewed, providing less confident insights.

9.1. Continuous Stimulation Reduces Arousal Level in Infancy – In a series of studies published from 1966, Yvonne Brackbill have demonstrated that various kinds of monotonous, continuous stimuli lead to an immediate reduction in infantile vigilance [140-5]. In the first 1966 study by Brackbill et al. [140], continuous auditory stimuli of three types were used with both neonates and ~2.8 years old infants (24 subjects of each group). In both groups, each type of auditory stimuli (1.2 Hz heartbeat, 1.2 Hz metronome, lullaby in a foreign language) lead to similar significant reductions in crying rate, heart rate and motor activity, with respect to ambient noise conditions. Some earlier literature is reviewed by the authors, reporting unexplained reduced arousal level in infants under continuous auditory, visual or kinesthetic stimuli. The authors also cite a 1922 remark of Ivan Pavlov, that in dogs: “Every monotonous and continuous stimulation leads to drowsiness and sleep” [v].

The soothing effects of a heartbeat stimuli were later confirmed in neonates [148], while invalidating a prediction that neonates would be better soothed by their own mother's heart rate, compared with an unfamiliar heart rate. These findings argue against an explanation, known as “Salk's Hypothesis”, which attributes the soothing effect of heartbeat stimuli to its resemblance to in uterus sensations.

In a subsequent study [141], Brackbill investigated the effects of continuous and intermittent auditory stimuli on the arousal level of sixteen one-month old infants. Auditory noise at 85 dB was used as a continuous stimuli, background 70 dB noise was used as control conditions, and alternate half-second periods of 85 dB and 70 dB noise were used as intermittent auditory stimuli. The arousal level was significantly decreased by the continuous stimuli and increased by the intermittent stimuli, relative to the control conditions. Specifically, the continuous stimulus has significantly increased the amount of time spent in quiet sleep, while reducing the time spent in active sleep and entirely eliminating crying. The intermittent stimuli also decreased the amount of time spent in active sleep, sharply increasing the time spent crying to 26% of the entire session. These findings strongly suggest that the continuous nature of the stimuli is essential for its soothing effect.

Interestingly, the soothing effect of continuous auditory stimuli on neonates was later found to increase with stimulus intensity [145]. That is, 80 dB white noise increased the time spent in quiet sleep more than 70 or 60 dB white noise, compared to an ambient noise level of 55 dB (see figure 34). Brackbill thus suggested that the continuous stimulation raises the sensory threshold, thereby reducing the flux of sensory input.

Brackbill also studied the effects of continuous stimuli in additional sensory modalities [142,144]. 85 dB 1.2 Hz heartbeat served as an auditory stimulus, versus an ambient noise level of

Figure 34: Percentage of time spent in quiet and active sleep and awake, as a function of continuous sound intensity. Scanned from [145].
62 dB. 400 W illumination served as a visual stimulus, versus 50 W illumination during control sessions. Swaddling the infant tightly from neck to toes using three ounces of flannel strips served as a proprioceptive-tactile stimulus, whereas extra clothes of the same weight served as control. Finally, 31°C and 25.5°C served as experimental and control temperature stimuli, respectively. Each of the four kinds of continuous stimuli had a marked pacifying effect on 24 one-month old infants [142]. This effect was manifested by a decrease in heart rate and irregular respiration, a decrease in gross motor activity and crying, and an increase in the amount of quiet sleep. Swaddling in particular was reported to produce a dramatic effect, diminishing crying and inducing sleep. The effect was cumulative across modalities – the more sensory modalities were continuously stimulated, the lower was the arousal level reached. In a subsequent similar experiment [144], the effect was shown to endure over a two-hour experimental session, with no clear signs of habituation.

Brackbill has been careful to emphasize, that it is unknown how the effect of continuous stimuli is mediated. She has suggested, though, that the effect does not depend upon the presence of a cortex. This suggestion is based on ten experimental sessions conducted with a single anencephalic infant at the age of ninety days. The subject had an intact cerebellum and brain stem but no telencephalon, consequently exhibiting a predominantly parasympathetic autonomic tone (see [143] for further details). According to [142], swaddling this subject lead to a significant decrease in mean heart and respiration rates: 84.49 vs. 90.06 b.p.m. and 28.51 vs. 31.34 b.p.m., respectively. Brackbill thus suggested that the stimulus-induced change in arousal level “is not an adjunct of some cognitive, cortically mediated function but is instead the product of a primitive, subcortical mechanism”. If the same sub-cortical mechanism is also responsible for the effects of rocking stimuli, it may make the hypothesis discussed in this survey somewhat redundant. Two possible points of weakness are therefore remarked: First, the subject has been reported to have a variable respiration rate and a widely fluctuating pulse rate [143], restricting the statistical significance of the said results. Second, the subject lived past the age of five months, whereas life expectancy for born anencephalic infants is about a few hours, suggesting a less severe case of anencephaly. The absence of cortical functionality in this subject is supported, among else, by his apparent lack of habituation to a recurrent stimuli (noise burst), reported in [143].

The following neurophysiological explanation is proposed in a later study [145]: “Sensory impulses pass up to the midbrain via specific sensory nerves, enter the reticular activating system via collaterals, continue on to the nonspecific thalamic nuclei, and to the orbital cortex. […] the most obvious component in this hypothetical sequence is the reticular activating system, and within the reticular activating system one might speculate that stimulation of the more dorsal raphe nuclei plays a prominent role in the effect. At the biochemical level, involvement of the raphe nuclei (and their heavy concentration of serotonin [Jouvet 1969]) would fit well with the data from all studies in this series showing that the most consistent state change is the marked increase in quiet sleep under continuous stimulation”. While the soothing effect of continuous stimulation are mentioned in a later review article on sleep [116], no later article I found cites or discusses this explanation. One introductory note at a 1997 paper [115] cites an explanation reminiscent of it for the soothing effects of rocking stimuli, as we shall see in the next subsection. This similarity may merely derive from the involvement of the raphe nuclei in the onset of sleep.

9.2. Rocking Stimulation Reduces Arousal Level in Infancy – Two 1973 studies by Pederson & Ver Trugt have investigated the effects of vertical rocking stimulation on the activity of two-month-old infants [146-7]. In both studies, infants were rocked for fifteen minutes in a bassinet at one of five frequencies in the 0.5-1.5 Hz range. Their activity was judged by observers every fifteen seconds, using a 1-6 numerical scale (1 – ‘quiet sleep’, 4 – ‘awake and restless’). Rocking magnitude corresponded to r.m.s. accelerations of 0.25-3 ms². Three experiments are reported in [146] and one
in [147], conducted with 42, 48, 44 and 64 two-month-old infants, each stimulated at a single rocking frequency (or none).

In all four experiments, the rocked infants became less active with time, whereas those left in the bassinet without rocking became more active with time. The mean observed activity during the last five minutes of rocking is seemingly proportional to the acceleration magnitude:

![Figure 35: Mean observer ratings during the last five minutes of rocking, as a function of maximum acceleration. The first number of each pair is the frequency in cycles per minute, and the second is the amplitude in inches. X axis adapted to the metric system. Scanned and adapted from [146].](image)

Apparently, rather intense vibrations (> 2.5 ms\(^{-2}\)) still had an increasingly soothing effect over the infants, with no clear sign of saturation or preference to a specific rocking frequency. These results are surely qualitative only, considering the activity estimation method applied in these studies. Ten minutes after termination of the 1.5 Hz rocking stimulus, the mean observed activity was significantly lower (p<0.01) than that observed in the control group [147].

As the rocking stimuli at different frequencies were not matched for acceleration magnitude, one cannot confidently tell whether frequency or sheer acceleration magnitude played a role in soothing the infants, thus further experiments are clearly required to quantify and qualify the observed effect. In a control experiment, eight infants were exposed to the sound of the rocker operating at 1.5 Hz. Those infants became significantly more active, a finding which argues against a soothing effect of the auditory stimulus alone [147].

In a 1982 review dedicated to the soothing effects of various forms of stimulation [149], Schaper cites three studies from the 1960s investigating the effects of rocking in infants. Gordon & Foss [vi] reported that rocking reduces the incidences of crying among newborns. Ambrose [vii] built a machine called a “vestibulator”, vertically rocking babies in a constant frequency. Reportedly, all infants tested stopped crying within fifteen seconds of rocking. Pederson et al. [viii] reported that “vigorous vertical rocking is more effective in quieting an infant than is horizontal, or back and forth, rocking” [149].
Barnard & Bee [150] exposed 59 pre-term infants to a combined stimulation of heartbeat sound and a bed rocker. The rocking stimuli consisted of 0.5 Hz vibrations at an acceleration magnitude of 0.38 ms\(^2\), whereas the frequency of the ~80 dB heartbeat was not specified. All 59 experimental infants, compared to 28 controls, showed decreased rates of activity, fewer abnormal reflexes and better orienting responses. A significant difference in infantile activity was found within four days of stimulation, sustaining over time into the 34\(^{th}\) week of the experiment. By the age of two years, the experimental group exhibited a significantly higher IQ score. No significant difference was found, between infants who were exposed to fixed 15 minutes of stimulation every hour, and those exposed to 15 minutes of stimulation whenever exhibiting no motor activity for ninety seconds. Therefore, there was no apparent long term effect for the learning task embedded in the conditioned stimulation. The authors suggest that there may be two effects produced by the given treatment: “The first effect, which we see in the immediate lowering of activity levels and shortened cycles, is directly attributable to the “soothing” quality of the rocking bed\ heartbeat sound. Perhaps the infants are lulled in some fashion so that they are simply quieter. But there may be a subtler effect as well, a kind of “programming” of the central nervous system that is not reflected in the child's behavior until at least age 2, when measurements of the child\'s cognitive capacity begin to be more heavily language dependent, and when more complex levels of cognitive tasks are included. Thus by assisting the infant to suppress activity, through both the lulling quality of the stimulation and the temporal regularity or contingency of the stimulation, we may have aided the developmental of crucial, but subtle, aspects of the central nervous system”.

Malcuit et al. [151] investigated the effects of lateral cradle rocking on infants at the ages of 1 and 3 months. Rocking frequency was either 1.2 Hz (“rapid rocking”) or 0.1 Hz (“slow rocking”), with an unclear acceleration magnitude. Of 47 infants participating in this study, 5 were excluded due to technical problems and 16 due to crying, leaving 26 infants who remained alert and calm during twelve trials. To my untrained eyes, such a sweeping exclusion is detrimental to the significance of the reported findings, which were anyway hard to comprehend and apparently non-innovating.

Chen-Hsing Lu et al. [115] developed an electronically controlled swinging cradle (0.4-1 Hz) meant to improve the sleeping of newborn infants. They denote that: “It is shown in the literature [116-8, ix, LG] that swinging can cause a phasic event that excites the semicircular canal system to produce natural wave signals which, in turn, stimulate the raphe system of the brain through the vestibular nerve and ganglion. With proper swinging, the generated stimulation can relax a person and make him fall asleep quickly”. I have read three of the four references provided in relation to these sentences [116-8], but failed to see their support to this assertion. The explanation suggested by Brackbill in [145] is somewhat reminiscent of this assertion (see 9.1 above), which is expectable due to the involvement of the raphe nuclei in the onset of sleep.

Most recently, Jahromi et al. [152] investigated the effectiveness of various methods used by mothers to regulate the response of their infants to an inoculation. In this longitudinal study, 141 infants were observed at the age of two months and 133 infants at six months. Eight distinct soothing behaviors were observed, of which 'holding\ rocking' was classified as "picking up the infant, with or without any movement". In both age groups, holding\ rocking was the most frequently observed maternal behavior, used in more than 80% of the observed time. Holding\ rocking and vocalization were revealed to occur more often in combination than independently, and this combination of behaviors was most effective at significantly reducing all levels of infant distress. These behaviors by themselves were associated with decreases in crying less often than expected by chance. Thus, holding\ rocking and vocalization behaviors were only found effective when occurring together. The authors suggest that the holding\ rocking begins the process of attention regulation, and that vocalization continues this process by maintaining attention. Further categorization of the behaviors
titles as 'holding\rocking' may help determine whether rocking in particular has a clear soothing effect, with or without vocalization.

All in all, there is a substantial body of evidence reporting the soothing effects of rocking on infants. According to [150], prolonged exposure to rocking stimuli might thereby have long term implications on the cognitive development of infants, at least in the case of hospitalized pre-term infants. Experimental evidence is too sparse to determine the optimal rocking stimulus conditions, which could have been useful in determining how rocking elicits sleep in infants. We learn from [150] that this phenomenon was unexplained by 1983, and fail to comprehend the explanation brought in [115] by 1997. The lack of recent quantitative experimental evidence is rather surprising, and is hopefully a mere outcome of my personal inexperience.

9.3. Infantile Colic and Motor Vehicle Vibrations – Infantile colic is generally defined as crying for more than three hours per day, for more than three days per week, for more than three weeks, in an otherwise healthy infant [153-5]. Despite numerous studies on this distressing problem, its cause remains unclear. The fact that most infants outgrow colic by four months, with no known after effects, supports a neuro-developmental cause of colic [153]. One commercial firm, Sweet Dreems Inc., sells a device that vibrates the infant's crib to stimulate the action of a car traveling at 88 km/h [155]. This device was shown to be as effective as placebo in improving colic symptoms [153-4], a fact not mentioned at the company website (http://www.colic.com/Effectiveness.htm). Another commercial crib vibrator was proven as ineffective in treating colic as infant massage [154]. Unfortunately, I didn't find any study investigating the possible soothing effects of these vibrators on healthy infants, nor any spectrogram of the vibratory stimuli they produce. It was shown though, that increased carrying reduces the crying time of healthy infants, but not of colicky infants [153]. We may thus expect crib vibrators to be efficent in soothing healthy infants, in accordance with the findings reported in the previous subsection.

That healthy infants are soothed by rocking and colicky infants aren't, suggests a link between the unknown cause of colic and the unknown mechanisms mediating the soothing effect of rocking. This link is hard to verify until the reason for either phenomena is elucidated.

9.4. Vibroacoustic Therapy – Vibroacoustic stimulation is a widely used clinical method to elicit a response in human fetuses. In this method, an electronic artificial larynx, with a vibrating disc attached to the maternal abdomen, delivers 60-70 Hz sound for several seconds, at a sound pressure level of 60-120 dB (measured in air) [156]. Vibroacoustic therapy is something completely different [157-9]. It is a therapeutic method developed through the 1980s by Olav Skille to treat children with various physical and mental disorders. In this method, sinusoidal vibrations in the 30-120 Hz range are delivered to a seated person, accompanied by relaxing music [157-8]. While seemingly effective in eliciting relaxation amongst disadvantaged persons, its field of research apparently suffers from several proto-scientific symptoms. Its origin is clearly pseudo-scientific [159], with no professional certification or training required to use vibroacoustic equipment [158], and most publications in the field being non-peer-reviewed. I haven't found any study using neuroscientific tools while applying vibroacoustic therapy. I therefore put aside for the moment this ambiguous source of clinical evidence, noting only that ~40 Hz vibrations were found especially effective in treating children [157]. Possibly any given effect of vibroacoustic therapy may be mediated by audiotactile interactions (see section 6.1 above), prompting for caution in its interpretation.

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10Excessive flatus was found to be an outcome rather than the reason of excessive crying.
10. Developmental Aspects of Neural Oscillations

This section was added once I realized that the differences between the EEG/MEG spectra of adults and infants may inflict on the hypothetical modulation of their brain activity by vibrotactile stimuli. Attention is directed only at these differences, ignoring findings in elderly people. My reading for this section has been less extensive, hence it's more likely that I missed some important findings and misinterpreted others.

10.1. Developmental Changes in EEG/MEG Spectra – The EEG [46] and MEG [33,46] power spectra of sleeping newborns is notable for its featureless 1/f distribution. About seven weeks after birth, a ~13 Hz peak appears in their MEG power spectra during quiet sleep, along with an increase of activity in the 0.5-3 Hz slow & delta bands [33,128-9]. This spectral combination corresponds to the emergence of spindle oscillations, a unique kind of neural oscillatory activity that we shall review in subsection 11.5. These are the only noticeable features in the MEG power spectra of sleeping babies, up to the age of six months, as probed in [33].

Multiple EEG [53,76,125-7] and MEG [35] studies have confirmed that the frequencies of alpha-band rhythms (occipital alpha, Rolandic mu, and possibly auditory tau) increase with age. A precursor of the occipital alpha rhythm emerges around the age of four months at ~4 Hz [53,125]. Like the adult rhythm, it vanishes with eye opening and reappears with eye closure. Its peak frequency rapidly rises to 6.2±0.5 Hz at 8 months, 6.8±0.4 Hz at 11 months [126], and ~8 Hz at 4 years [53,76]. Accordingly, the frequency of the Rolandic mu rhythm rises from 7.0±0.5 Hz at 8 months to 7.4±0.5 Hz at 11 months [126] and ~9 Hz at 4 years [53]. Stroganova et al. speculate that the ~0.6 Hz difference between the Rolandic mu rhythm and the occipital alpha rhythm, which is preserved into adulthood, stems from in utero somatosensory stimulation, which obviously has no visual counterpart until birth [126]. Individually higher EEG power densities of ~6.8 Hz occipital alpha and Rolandic mu rhythms were significantly correlated with the ability of infants to maintain attention, at the age of 8-11 months.

Two studies [126,127] report the presence of ~4.5 Hz EEG activity over multiple electrode sites in 8 and 11 months old infants, which could be a precursor of the adult 4-8 Hz theta rhythm. While further evidence is needed to corroborate this finding, it is clear that both the much stronger 6-8 Hz activity in children than in adults, and its pronunciation towards occipital sites, agree with its suggested role as a precursor of the adult ~10 Hz occipital alpha rhythm [34]. The frequency of alpha band rhythms (and possibly theta as well) settles by the age of late adolescence (~16). It is noteworthy that the frequencies of other neural rhythms (beta, gamma, slow, delta, spindle) do not change with time, with only their amplitudes and distribution evolving with age. I haven't found any studies suggesting an explanation for this discrepancy.

Gamma band activity is observed within the age of eight months [80], or even six months [82]. It is enhanced during visual cognitive tasks with temporal and spatial patterns similar those observed in adults, suggesting a similar functional role in binding information [80, debated in 81].
Without sinking too deeply into details, we can note the following developmental changes:

<table>
<thead>
<tr>
<th>Frequency (Hz)</th>
<th>Band Name</th>
<th>Developmental Change</th>
<th>Age of Maturation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.3-1</td>
<td>Slow</td>
<td>Decrease</td>
<td>None</td>
<td>35,55</td>
</tr>
<tr>
<td>1-4</td>
<td>Delta</td>
<td>Decrease</td>
<td>None</td>
<td>35,55</td>
</tr>
<tr>
<td>4-6</td>
<td>Slow Theta</td>
<td>Decrease</td>
<td>~12</td>
<td>34,35,53,76</td>
</tr>
<tr>
<td>6-8</td>
<td>Fast Theta</td>
<td>Increase</td>
<td>~4</td>
<td>53</td>
</tr>
<tr>
<td>8-10.5</td>
<td>Lower Alpha</td>
<td>Major Increase</td>
<td>~12</td>
<td>35,53,76</td>
</tr>
<tr>
<td>10.5-14</td>
<td>Upper Alpha</td>
<td>Increase</td>
<td>~16?</td>
<td>35,53,76</td>
</tr>
<tr>
<td>14-30</td>
<td>Beta</td>
<td>Increase</td>
<td>?</td>
<td>35</td>
</tr>
<tr>
<td>30-80</td>
<td>Gamma</td>
<td>Increase</td>
<td>~40?</td>
<td>32,35</td>
</tr>
</tbody>
</table>

Here 'age of maturation' denotes the age from which the earlier developmental trend becomes smaller than standard deviation. There are finer details involved, but we may crudely say that neural activity above ~10 Hz increases with age, with an opposite trend for neural activity below ~10 Hz.

10.2. Developmental Changes in ASSR – The ASSR in the first few months of life are 3-5 dB lower in magnitude than adult ASSR [119]. More complex modulation techniques are used to elicit ASSR in infants, employing multiple spectral components [37,119]. In stark contrast to adult ASSR (see section 2.1), infants do not exhibit an increased responsiveness to 40 Hz stimulus [32,37]. Recently, Riquelme et al. [37] performed an ASSR study with a large sample of 149 newborn babies. Their ASSR amplitudes have smoothly declined with stimulus frequency in the 25-98 Hz stimulus frequency range. Citing the authors: “Certainly, adult modulation transfer functions differ from those in infants in that a peak at 40 Hz is only prominent in adults”. In another recent article, Rojas et al. [32] have probed the 40 Hz MEG ASSR in 69 subjects ranging in age from 5 to 52 years. Most subjects exhibited a peak spectral power at 40 Hz, its mean amplitude increasing with age. There were large inter-individual differences in ASSR amplitude, possibly related to subjects’ alertness, but particularly high ASSR were only observed beyond the age of twelve or so. Considering the absence of ~40 Hz gamma band activity in newborn infants [80-82], this finding suggests an interlink between the intrinsic gamma band activity and 40 Hz ASSR.

I have not read ASSR studies in children probing stimulus frequencies lower than 25 Hz. Neither have I found developmental ASSR studies investigating the EEG/MEG response frequencies as a function of stimulus frequency (as done with adults in [50]). Relevant literature is abundant though, and further search may yield just that later on.

10.3. Developmental Changes in SSVER – Birca et al. [76] measured the SSVER of 41 children ranging in age from 3 to 16 years, and ten adults. The stimuli frequencies were 5, 7.5, 10 and 12.5 Hz. Importantly, the authors distinguished between the spontaneous pre-stimulus EEG spectra, SSVERs and the ongoing (undriven) EEG spectra. Their resulting mean values of the dominant spontaneous frequency and preferred resonant frequency (i.e. stimulus frequency in which SSVER amplitude was highest) are summarized in the following table:

<table>
<thead>
<tr>
<th>Age groups (N)</th>
<th>Male/female ratio</th>
<th>Dominant resting EEG frequency (SD)</th>
<th>Preferred resonant frequency (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-5 years (11)</td>
<td>6/5</td>
<td>8.2 (0.88)</td>
<td>8.2 (1.89)</td>
</tr>
<tr>
<td>6-9 years (10)</td>
<td>4/6</td>
<td>9.2 (0.64)</td>
<td>6.3 (1.89)</td>
</tr>
<tr>
<td>10-12 years (10)</td>
<td>5/5</td>
<td>10.5 (0.95)***</td>
<td>9.3 (2.65)</td>
</tr>
<tr>
<td>13-16 years (10)</td>
<td>5/5</td>
<td>10.2 (0.78)***</td>
<td>9.3 (2.06)</td>
</tr>
<tr>
<td>21-41 years (10)</td>
<td>5/5</td>
<td>10.1 (0.60)***</td>
<td>9.4 (2.43)</td>
</tr>
</tbody>
</table>

Table 2 - Demographic characteristics of the participants and mean values of the dominant spontaneous EEG and preferred resonant frequency, according to age. *** denotes a p<0.001 level of significance for differences between the youngest and each of the older age groups. Copied from [76].
old children. As remarked by the authors, age effects may be present in younger children (less than 3 years old), at higher frequencies or with a larger number of subjects. Nevertheless, undriven alpha activity is suppressed during rhythmical visual stimuli, and its mean frequency is positively correlated with age, as evident from table 2.

I have not read SSVER studies in children probing stimulus frequencies higher than 12.5 Hz. However relevant literature is once again abundant and further search may be fruitful.

10.4. Developmental Changes in SSVER? – I have found a single 2004 study by Pihko et al. [46], demonstrating that it is possible to record somatosensory evoked potentials in sleeping newborn infants. As this study claims to be the first of its kind, there is good reason to believe no SSVER studies were done with children yet. Using both EEG and MEG, the authors found differences between the somatosensory evoked responses elicited during active sleep and quiet sleep. These findings are further discussed in a 2004 review by Pihko and Lauronen [48]. Specifically, a response compatible with SI activation was more clearly identified during quiet sleep. Interestingly, their EEG and MEG power spectrograms reveal higher activity in the 0.5-1 Hz and 10-15 Hz bands during quiet sleep than during active sleep. We shall discuss this suggested finding in section 11.5 below. I have found no other relation of their findings to my context of interest.
11. Candidate Modulated Neural Rhythms

In this section we shall review the various neural rhythms that might be modulated by motor vehicle vibrations. These candidates are not mutually exclusive, but some seem more likely than others. The underlying assumption is that at any given age, only existing neural rhythms may be entrained. For instance, it is assumed impossible for a ~10 Hz alpha rhythm to appear in the EEG spectrum of an six-months-old infant, as the frequency of his/her alpha rhythms is expected to be ≤6 Hz (see subsection 10.1 above).

11.1. Alpha Oscillations (7-14 Hz adult, 4-11 Hz infantile) – 7-14 Hz alpha band oscillations are the most prominent spontaneous EEG\MEG activity observed in awake adults [53,76]. It is most pronounced over the occipital and parietal regions, gradually decreasing in amplitude towards the anterior cortical areas. Higher activity in the alpha band is correlated with tiredness and sleep deprivation, but not with drowsiness and sleep [55,138,161]. Various cognitive tasks requiring attention also elicit an increase in alpha activity [126-7,138-9, 193-5]. A novel interpretation is thus suggested. We suggest that increased alpha activity is a marker of many attention-demanding states, including 'fighting with sleep'. When one wants to stay awake and alert despite being tired, his/her alpha activity increases.

This interpretation seems to be compatible with the existing experimental evidence [55,126-7,138-9,161]. I do not recall an earlier study suggesting it, though it is not all that different than the present views over the alpha rhythm, i.e. those replacing the outdated 'idling hypothesis'.

The effects of prolonged wakefulness on both the sleep and wake EEG are most pronounced in frontal cortical areas of the brain [55]. According to a recent enlightening rat study [31], this frontal enhancement of alpha activity may be an manifestation of the Rolandic mu rhythm. A 7-12 Hz rhythm has been identified in rats and compared to the human somatosensory mu rhythm [31]. Neuronal ensembles in the medial prefrontal cortex (MPC) exhibited a high degree of synchrony in their firing rates during 7-12 Hz oscillations, that is not exhibited in other conditions. Moreover, these 7-12 Hz oscillations were frequently preceded by an awake state and followed by slow wave sleep, accompanied by shorter bursts of <4 Hz slow wave activity. Last but not least, this 7-12 Hz activity was enhanced when following prolonged periods of wakefulness. All these findings suggest that the rat analogue for the human somatosensory mu rhythm is also involved in the transitional state between the awake and sleep states [31]. In fact, its pattern resembles that of 13 Hz sleep spindles observed during light sleep in adult humans [164]. We shall further discuss the possible linkage between the human mu rhythm and spindle oscillations in subsection 11.5.

Ostensibly, these rat findings could lend support to the suggestion, that the entrainment of the Rolandic mu rhythm could be reflected into cortical regions involved in higher cognitive functions, such as the medial prefrontal cortex. Romo et al. [9,10,13] have indeed found that information about the frequency of a past vibrotactile stimulus was maintained in prefrontal neurons, in a monkeys' working memory task (see section 4.2 above). Yet this does not imply that entire prefrontal neuronal ensembles are synchronized with the Rolandic mu rhythm, not even if this rhythm is concurrently being modulated by vibrotactile stimuli. Moreover, the human mu rhythm is mostly observed during wakefulness and REM sleep, and not during slow wave sleep [47]. A single paper [125] demonstrated that it is the mid-temporal tau rhythm [64,65,125], and not the Rolandic mu rhythm, that is occasionally observed during slow wave sleep. Thus strong evidence is required to apply these interesting rat findings to humans.

Notwithstanding the unclear relationship between the Rolandic mu rhythm and the onset of sleep, there is good reason to believe this rhythm may be entrained by whole-body vibrations. The preliminary EEG and MEG findings reviewed in section 5 strongly suggest that pre-stimulus activity...
in the alpha band is somehow modulated by ~10 Hz vibrotactile stimuli. Considering the developmental increase in the frequency of alpha rhythms (see section 10.1), we expect that infants should be more susceptible to ~4-11 Hz vibratory stimuli, depending on their age. Towards the age of one year, the individual frequency of the mu rhythm is expected to match the whole-body vibrational resonant frequency, as measured in [24] (see section 7.3). Accordingly we suggest that infants at this age group should be most susceptible to entrainment of their neural alpha activity by whole-body vibrations. One drawback in this prediction comes from SSVER measurements in children and adults [76], in which no correlation was found between the dominant spontaneous alpha frequency and the stimulus frequency in which SSVER amplitude was highest. Experiments may test this prediction and hopefully lay basis for better theoretical reasoning [199].

Bearing in mind the non-linear susceptibility of alpha oscillations to rhythmical auditory, visual and possibly somatosensory stimuli, we expect the ~10 Hz alpha activity of adults to be modulated by vibratory stimuli at frequencies other than ~10 Hz. As the resonant frequency of human adults to whole-body vibrations is about 5-6 Hz (see section 7.3), an harmonic entrainment of ~10 Hz alpha activity is suggested. According to one SSVER study [95], entrainment of ~10 Hz activity by 5 Hz stimuli is weaker than that achieved by 10 Hz stimuli, but also less sensitive to the subject's mental and physical conditions. As discussed in section 5.2 above, the present evidence for such non-linear modulation of alpha activity is rather sparse, thus further experimental evidence is clearly required.

All in all, alpha oscillations are a leading candidate for modulation by motor vehicle vibrations. We cannot confidently point out the expected effects of such a modulation on cognitive performance and vigilance level. The fact that rocking stimuli soothes 0-6 months old infants [146-152] argues against the involvement of alpha band modulation in the neural process underlying this soothing effect.

11.2. Beta Oscillations (~20 Hz) – As we saw in subsections 4.6-4.8, somatosensory processing is associated with induced synchronous beta oscillations in the primary and secondary somatosensory cortices. Moreover, 20-27 Hz sinusoidal vibrotactile stimuli evoked marked EEG activity at the stimulus frequency over central electrode sites [18,27,28,42,i], as we saw in subsection 5.2. This finding may be an outcome of the entrainment of evoked beta oscillations by the vibrotactile stimulus. Alternatively, it may be an outcome of the stronger spontaneous activity recorded in lower frequencies, as part of the 1/f spectral distribution of neural electrical activity. Once future SSSER studies investigate the induced and undriven components of the neural response to vibrotactile stimuli, the two interpretations could be tested.

Seated human passengers are less susceptible to whole-body vibrations in the 15-25 Hz frequency range than to vibrations at lower frequencies (see section 7.3 above). Moreover, periodic vibratory sensations at lower frequencies are expected to be better enhanced via stochastic resonance than those at higher frequencies (see section 4.9 above). 16 Hz whole-body vibrations were reported to have a detrimental effect on cognitive performance [iii,iv], a finding later controverted using a larger sample size [100].

In conclusion, beta oscillations are a less promising candidate for modulation by motor vehicle vibrations, though this option certainly cannot be ruled out yet.

11.3. Gamma Oscillations (~40 Hz) – Neonatal ASSR measurements [37] suggest that specific responsiveness to 40 Hz auditory stimulation is absent in newborn infants, probably due to lack of observable gamma band activity before the age of six months. Accordingly, we expect that 40 Hz vibrotactile stimuli should not elicit a unique neural response in infants, at least before they're ~6 months old. Responsiveness of older infants to 40 Hz vibrotactile stimuli should be weaker, on average, than that of adults. This prediction holds especially if such hypothetical vibrotactile neural
modulation occurs only via the audiotactile path (see section 6.1). The fact that rocking stimuli soothes 0-6 months old infants [146-152] strongly suggests no involvement of gamma band activity in the neural process underlying this soothing effect.

11.4. Slow Oscillations (0.3-1 Hz) and Delta Oscillations (1-4 Hz) – Three neural rhythms are exhibited during slow-wave sleep: 0.3-1 Hz slow oscillations, 1-4 Hz delta oscillations, and 7-15 Hz spindle oscillations [121]. The slow oscillation is a cortical rhythm, recorded in all major types of neocortical neurons, including pyramidal neurons [121]. It originates in anterior frontal regions, propagating in an anterior-posterior direction. In contrast, delta oscillations have both a thalamic and a cortical component [121-2]. Delta and spindle oscillations are always superimposed on the depolarizing (“up”) phase of the slow oscillation. Similarly, when beta and gamma oscillations briefly appear during slow wave sleep (associated with rational, repetitive dreams), they are superimposed on the depolarizing phase of the slow oscillation [121].

Higher 0.3-1 Hz EEG activity is positively correlated with sleep deprivation [55,121] and negatively correlated with age [55], while delta oscillations occur more frequently as sleep deepens [121-2,161]. A slow-wave complex is a remarkably synchronized network event, in which a concerted period of silence is seen across the network, followed by a rebound firing in most of the cells [123]. There is experimental evidence supporting the hypothesis that the slow oscillation is responsible for the consolidation of memory traces acquired during the state of wakefulness [121,123]. Among else, a local ~27% enhancement of slow wave activity was found two hours after a motor learning task, localized to parietal areas receiving visual and proprioceptive inputs relevant to spatial attention and skilled action [121].

As we saw in subsection 9.2, rocking stimuli at 0.5-1.5 Hz was found effective in soothing infants. Present experimental evidence is inadequate to determine whether 0.3-4 Hz vibrations are more (or less) effective soothers than other frequency bands, or is it the sheer magnitude of rocking acceleration that counts. Motor vehicle vibration power spectrograms do not contain any specific peak at 0.5-4 Hz.

Slow, delta and spindle oscillations are first observable in the EEG\MEG spectra of sleeping infants by the age of ~7 weeks [33,128-9], as we learned in subsection 10.1. Therefore, the fact that rocking stimuli soothes newborn infants [149-150] argues against the involvement of the three sleep rhythms in the neural process underlying this soothing effect. Then again, at present we cannot overrule the possibility, that the averaged amplitude of these rhythms at birth is too weak to be picked up by EEG\MEG. This suggestion is supported by the neonatal EEG and MEG power spectrograms provided in [46], which reveal higher activity in the 0.5-1 Hz and 10-15 Hz bands during quiet sleep than during active sleep. This might indicate the presence of K-complex (slow oscillations + spindling) activity in three-day-old neonates, during quiet sleep. It is worth investigating whether rocking may stimulate an earlier pronunciation of sleep rhythms (slow, delta and spindling) in neonates.

11.5. Spindle Oscillations (7-15Hz) – Spindle oscillations most frequently appear during the onset of slow-wave sleep (stage 2), and during transitions between REM and slow-wave sleep [33,121-3,161-5]. Spindles are 7-15 Hz oscillations, organized within an envelope of 0.5-0.7 Hz slow oscillations, lasting for 1-3 seconds and recurring periodically every 10-20 seconds [123,164-5]. This combination of slow and spindle oscillations is termed the K-complex, and is also apparent in other stages of slow-wave sleep [121,161]. Spindle oscillations are generated in the thalamus, paced by thalamic reticular neurons, and synchronized by the cerebral cortex [121-3]. Thalamic rCBF decreases dramatically as a function of K-complex activity, reflecting the active inhibition of thalamocortical neurons during slow-wave sleep [161].
Spindle oscillations elicit a very high degree of coherence (>80%) in neural activity across broad regions of the frontal, central, parietal and occipital cortices [123,165]. They play a fascinating role in synaptic plasticity and memory consolidation during sleep, as lucidly elaborated in [121,123]. To cite but two related findings, the density of human sleep spindles is significantly higher after training on a declarative learning task, and also after auditory stimulation, after which an increased coherence is found between frontal and temporal cortical regions [121]. This functional role appears to be more founded than the sleep-maintaining role suggested in some clinical studies, as blockers at the thalamic level of sensory information transfer into the cerebral cortex [163-6].

EEG/MEG recordings of spindle oscillations reflect the activity of cortical pyramidal neurons, and not of the thalamic neurons generating this rhythm [162]. Two kinds of spindle oscillations are identified in some clinical EEG/MEG studies, according to their peak frequency – 'slow' 10.5-12 Hz spindles and 'fast' 13-14 Hz spindles [162-3]. ~14 Hz spindles demonstrate a swirling sinusoidal activity, primarily at the midline superior parietal region of the scalp. Its location is extremely static and stable between and within subjects. ~12 Hz spindles are exhibited less often, with a much greater variability of location, amplitude, and voltage propagation across the scalp. The swirling dynamic topography of both kinds of spindles is illustrated by movies provided in [163] (see bibliography). Mircea Steriade objects the distinction between fast and slow spindles [121], as no functional difference between the two has been identified yet.

Considering the spatial proximity of the EEG/MEG sources of spindle oscillations and the Rolandic mu rhythm, and their similar frequencies (in adults), a connection between the two has been suggested in human [114] and rat [31] studies. A subsequent MEG study argued against this hypothesis [162], based on differing 'center of gravities' for the the two rhythms. Most recently [165], LORETA tomography revealed three distinct sources for spindle oscillations. Secondary and primary motor areas, as well as some cingulated areas (Brodmann areas 6,31,41,4/24), were identified as the primary source of spindle oscillations. Secondary somatosensory regions and posterior cingulated areas (BA 5,7) were identified as a second source. A third source composed of prefrontal regions and anterior cingulated areas (BA 10,32,42). A connection is thus suggested between ~14 Hz spindle oscillations and the specific regions involving control of movement.

Incidentally, a prominent ~13 Hz peak is observed in the vibratory spectra of traveling motor vehicles, as we saw in section 7.4. At present it sounds too far-fetched to suggest that rhythmical sensory stimulation at any frequency can elicit the generation of spindle oscillations. However, we speculate that rhythmical stimulation at ~13 Hz may synchronize emerging spindles, thereby assisting in sustaining the onset of slow-wave sleep. Future experiments may elucidate the feasibility of such a mechanism, localizing it either to cortical somatosensory sites or to thalamic sites. As seated infant passengers absorb ~13 Hz whole-body vibrations better than adult passengers (see section 7.4 above), we speculate that this hypothetical modulation is more prominent in infants.

As is the case with slow and delta oscillations, the fact that rocking stimuli soothes newborn infants [149-150] argues against the involvement of spindle oscillations in the neural process underlying this soothing effect. The same arguments promoted at the end of the previous subsection apply here.

11.6. Slow Oscillations in The Enteric Nervous System (0.05-0.3 Hz) – To this stage we have focused on the direct effects of whole-body vibrations on the central nervous system (CNS). Whole-body vibrations may also affect the enteric nervous system (ENS), later projecting on to the CNS.
A single rhythmical component is identified in normal gastric myoelectrical activity, with a frequency of 0.05±0.01 Hz [166-170,180]. Motion sickness is associated with higher frequencies of gastric myoelectrical activity, in the 0.06-0.2 Hz range, a state termed tachygastria or tachyarrhythmia, depending on its regularity [167-170,180]. The precise nature and reliability of the changes in the stomach's electrical activity during motion sickness are not clear, as either tachygastria or motion sickness may appear independently [180]. Normal ~0.05 Hz myoelectrical activity is positively correlated with sleep quality, whereas tachygastria activity is negatively correlated with it [168]. Tachygastria may be elicited by prolonged or temporary mental stress, such as that induced by an electrical shock stimulus [167]. It is also associated with increased sympathetic activity, which in turn influences the 0.04-0.08 low frequency component of the heart rate [167]. Though the infant's nervous system is plastic and developing [181], the same ~0.05 Hz frequency of normal myoelectrical activity is exhibited in pre-term and full-term neonates, with lesser amplitude [169]. All in all, the precise mechanisms that trigger and set the pace of gastric slow waves are unknown, at least as of 2003 [182].

Interstitial cells of Cajal play a vital role in the generation and propagation of gastric and intestinal myoelectrical activity [166,183-9]. These cells exhibit an oscillatory electrical activity at ~0.3 Hz [183-6], paced up to ~1 Hz by certain drugs in animal in vitro studies [184-5]. Canine and human studies have demonstrated that 0.05-0.3 Hz electrical stimulation may modulate the intrinsic 0.05 Hz gastric myoelectrical activity (see [166] for review). This prospective treatment was termed 'gastric pacing', 'gastric electrical stimulation' and finally 'neuro-modulation of vagal activity' [166,187]. The later term refers to the activation of the vago-vagal heart reflex during this treatment, indicating the effect of neuro-modulation on the circulatory center [187]. 50 Hz electrical stimulation of canine stomach [188] and colon [189] was also efficient in producing contractions, when applied sequentially over several electrode sites, within a slow temporal envelope.

Accordingly, one may expect the ENS to be more sensitive to mechanical vibrations at frequencies below 1 Hz, mostly in the 0.01-0.3 Hz range. Indeed, there are numerous studies linking motion sickness with low frequency (<1 Hz) oscillations (see [119] for non-exhaustive review), which suggests that the ENS is sensitive to whole-body vibrations. Unlike the homo-nucleic representation of somatic sensation, gut sensation is vaguely represented in the somatosensory cortices [181]. Therefore we expect that whole-body vibrations may cause tachygastria, thereby inducing feelings of discomfort and annoyance. As we saw in section 8.1, two studies reported feelings of discomfort elicited by whole body vibrations, with no apparent effects on cognitive performance [100-1]. These findings are compatible with a vibration-induced tachygastria. Modulation of ENS activity mechanical vibrations at higher frequencies is less likely, yet conceivable considering the rather intricate synchronization demonstrated between heart-beat and respiration [197].
12. Discussion

12.1. What I Haven't Found – The previous sections review the studies I have found of relevance for the purpose of this work. In some essential topics I have failed to find any relevant studies, which in some cases suggests no such studies were conducted yet. Here is what I haven't found:

1) EEG\MEG studies that demonstrate the modulation of ongoing neural activity by a rhythmical sensory stimulation, with an observed cognitive effect. Two groups reported such cognitive effects for auditory [41] and visual [78] stimuli, but apparently the only study that attempted to find EEG evidence for neural oscillatory entrainment [79] came up with puzzling results.

2) Neuroscientific studies investigating human brain activation during usage of massagers.

3) EEG\MEG SSSE studies with infants and children.

4) EEG\MEG SSSE studies conducted with vibrotactile stimuli delivered to any part else than the hand and sole.

5) EEG\MEG spectral analysis of the neural response to whole-body vibrations (let alone during concurrent working memory tasks).

6) EEG\MEG studies of infants and children undergoing whole-body vibrations.

7) Neuroscientific studies probing the possible cognitive effects of various frequencies of whole-body vibrations. I have only found studies using a single type of vibratory stimulus – either monochromatic [100,iii,iv] or dispersed [101].

8) Neuroscientific studies dealing with motor vehicle passengers.

9) Neuroscientific studies investigating why infants easily fall asleep in motor vehicles. This is despite the existence of at least one commercial product [155] purported to be based on this phenomenon.

As noted time and again through this survey, somatosensory research seems to lag behind its auditory and visual counterparts. I haven't found any specific technological limitations slowing down somatosensory research with respect to other modalities. Suggestively, this is plainly a matter of past increased interest in the other modalities that lead to their greater understanding. This leaves plenty of room for further insightful research on phenomena such as the hypothetical effects of vibratory stimulation discussed in this work.

12.2. Natural Frequencies of Different Sensory Systems – It has been suggested in earlier literature that each sensory modality has its own resonant frequency, for which the resulting response is greatest. The preferential “resonant” frequency is highly dependent on the definition of the desired response. Some studies define it as the stimulus frequency eliciting the largest EEG amplitude at its own rate [3,77]. Others look for the largest increase in amplitude at the stimulus frequency, so-called “highest SNR” [27,28]. Others sum the amplitude at harmonics of the stimulus frequency [18], but ignore any enhancement of subharmonic components. fMRI and PET studies lack the temporal resolution of EEG & MEG studies, looking instead for an overall increase in parameters corresponding to local neural activity. On top of all that, only rather recent studies [49,50,67,76] Distinguish between evoked and induced response, displaying the spectral distribution and “preferential frequency” of both activities.
Snyder [18] suggested 26 Hz as the resonant frequency of the somatosensory system, placing it between the visual 10-18 Hz and the auditory 40 Hz. Tobimatsu et al. [27,28] replicated this argument, setting the preferred somatosensory stimulus frequency at about 21 Hz, whereas Müller-Putz et al. set it at 27 Hz [i]. This modal segregation is of clinical use, as it directs us towards specific frequencies most useful for testing whether a patient still sees, hears or senses touch. However, it does not necessarily reflect an actual segregation between the resonant frequencies of different sensory modalities. Inter-modal similarities suggest a unifying point of view may be beneficial, as discussed hereunder.

12.3. **Inter-Modal Similarities** – Both the visual and auditory modalities are clearly sensitive to rhythmical stimulation at ~10, ~20, ~40 and ~80 Hz. Entrainment of 40 Hz gamma activity by either auditory or visual stimuli affects performance in concurrent cognitive tasks. Experimental evidence on somatosensory steady-state response is currently inadequate, yet clearly indicates that pre-stimulus activity in the alpha band is somehow modulated by ~10 Hz vibrotactile stimuli. At all three modalities, a spontaneous rhythm in the alpha frequency band is localized to the respective sensory areas – auditory tau rhythm, visual occipital alpha rhythm, and somatosensory mu and sigma rhythms. This rhythm becomes phase-locked to a sensory stimulation, its enhancement by harmonic or subharmonic stimuli sometimes exceeding the amplitude enhancement at stimulus frequency. At all three modalities, activity at lower sensory areas is time-locked to the eliciting stimulus remarkably well, whereas higher cortical sensory and prefrontal areas extract the signal envelope and preform complex manipulations upon it.

A unifying point of view is thus suggested. According to this notion, both alpha, beta and gamma neural oscillations may be modulated by rhythmical stimulation of each sensory modality. Modulation of locally synchronized oscillations yields a locally affected response. Modulation of oscillations synchronized over long cortical distances yields a globally affected response, such as increased or decreased vigilance. The somatosensory system may be unique in its increased reliance on synchronous beta band activity, yet it should also be susceptible to modulation of activity in the alpha and gamma bands. Further experimental evidence is required to assess the validity and applicability of this unifying notion. I take the experimental evidence reported in this survey to be compatible with this notion. It is also compatible with the hypothesis elaborated in a recent review [36], regarding the functional significance of the Rolandic mu rhythm.

Furthermore, similar methods of signal processing at different cortical sensory areas may make crossmodal interactions much easier to realize. In simple words, if all cortical sensory areas use the same language, it's easier for them to speak with one another. Otherwise, specific 'translators' are needed, adding latency, incompatibility and complexity to crossmodal interactions. The multi-modal nature of regions such as the posterior parietal cortex (PPC) [174-6] is congruent with this assumption.

12.4. **Dismissal of a Behavioral Argument** – Two conflicting behavioral arguments may be sketched. On the one hand, primate infants typically cling to their mothers as they move around. They are thus frequently exposed to whole-body vibrations, which are not particularly indicative of a situation demanding alertness or attention. Therefore there is no long-term evolutionary pressure against a soothing effect of mild whole-body vibrations upon infants. This argument in itself does not serve as any experimental evidence for the existence of such vibration-induced drowsiness. Even once experimental evidence is found, it still does not imply that it is derived from the suggested modulation of brain oscillations by sensations elicited by vibrations. Yet this argument could be used when asking why such a mechanism, once existing, is not suppressed in primate infants.
On the other hand, as primate infants are frequently exposed to whole-body vibrations at their resonant ~7 Hz frequency, neurological mechanisms suppressing brain activation elicited by these vibrations are likely useful. Such compensation mechanisms should be evident in the somatosensory and visual cortices, constantly enduring mechanical and image stabilization demands. I'm afraid both conflicting behavioral arguments should be dismissed as tautology, though my lack of background in behavioral science precludes making any confident assertion about it.

12.5. *Theoretical Points of Weakness & Alternative Explanations* – There are certainly several points of weakness in the hypothesis motivating this survey, some of which are hereby noted. The key point of weakness is the lack of theoretical understanding of steady-state responses to rhythmical sensory stimuli. ASSR & SSVER have been qualified on the phenomenological level, but their underlying mechanisms are currently unknown. The SSSER phenomenon has not been well qualified yet, let alone explained, especially in the context of whole-body vibrations. Therefore, this work only suggests an analogy between an untreated phenomenon (SSSER) and two other unexplained phenomena (ASSR & SSVER). That's more than nothing, but not enough.

The present evidence for the physiological and psycho-emotional effects of whole-body vibrations on humans, reviewed in sections 8 & 9, is compatible with a frame of work in which whole body vibrations modulate the ongoing brain activity. All the same, they cannot be taken as sufficient evidence for the existence of such a modulation. Instead, they may very well be explained by entirely different mechanisms in place of, or in addition to, this hypothetical modulation. Furthermore, any evidence for a cognitive effect of vibrotactile stimuli may possibly be explained by audiotactile interactions. Only concurrent use of neuroimaging tools may confirm the modulation of human neural oscillations by vibratory stimuli, and in turn tell the two modulation paths (somatosensory & audiotactile) apart to some extent.

Moreover, the reliance on vertical whole-body vibrations as a dominant source for vibrotactile stimulus deserves careful experimental inspection. Possibly, vibrations transmitted locally to specific body parts, at other frequencies than the whole-body vibration resonant frequency, may very well elicit a significant modulation of neural activity.

In section 11.6 we reviewed the possible modulation of enteric neural activity by whole-body vibrations, later projecting into the central nervous system. This possible path may have nothing to do with the entrainment of neural oscillations in the ENS or CNS, and its investigation may be hampered by the lesser capabilities of present ENS neuroscientific tools.

When specifically addressing the issue of passenger drowsiness in motor vehicles, there's an evident problem with inter-dependent variables. Newborn infants sleep for 18-22 hours per day [68], hence they're expected to be found sleeping anywhere, motor vehicles inclusive. Control experiments have to be carefully planned to avoid false identification of soothing effects. Similarly, drivers are prone to fatigue due to prolonged driving, regardless of motor vehicle vibrations, and decoupling the two effects may only be feasible in driving simulators. The drowsiness of commuters is likely predominantly influenced by sleep deficits and stress, while that of subway and airplane passengers is probably influenced by their exposure to lower oxygen levels. As a result, possibly existing studies on this comparable phenomena is inapplicable for this survey.

12.6. *Conclusions* – Motor vehicle vibrations elicit a multi-modal sensation, including somatosensory, vestibular, auditory and visual components. Its somatosensory component might modulate the ongoing neural activity, both directly via the somatosensory cortices, and indirectly via audiotactile
and visuotactile interactions. Intensive vibrations may also stimulate the enteric nervous system (ENS), later projecting to the CNS.

Cerebral neural oscillations in the alpha band (7-14 Hz for adults, 4-11 Hz for infants) are a leading candidate for modulation by motor vehicle vibrations. Their functional role is reinterpreted as associated with maintenance of alertness, to comply with their diverging experimental manifestations. For 1-2 years old infants, the peak frequency of alpha-band neural oscillations matches the frequency of peak power absorption of vertical whole-body vibrations. Accordingly we suggest, that infants at this age group should be more susceptible to entrainment of their neural alpha activity by whole-body vibrations. We cannot confidently point out the expected effects of such a modulation on cognitive performance and vigilance level.

The fact that rocking stimuli soothes 0-6 months old infants [146-152] argues against the involvement of alpha band modulation in the neural process underlying this soothing effect. Instead, we speculate that the ~13 Hz component of motor vehicle vibrations may lead to improved synchronization of 7-15 Hz spindle oscillations, thereby promoting sleep in infant and adult humans alike. Infants are better absorbers of ~13 Hz whole-body vibrations, which might suggest that the hypothetical modulation of spindle oscillations is more prominent in infants.

Existing experimental evidence is apparently too sparse to confirm or refute the hypothetical modulation of neural oscillations by temporally patterned sensations, induced by motor vehicle vibrations. Specifically, we don't know if this hypothetical modulation has anything to do with the underlying processes by which rocking elicits sleep in infants. Present-day technology enables performing insightful neuroscientific research, which will hopefully shed light on these fascinating phenomena.
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