Harmonic amplitude summation for frequency-tagging analysis

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Abstract

In the approach of frequency tagging, stimuli that are presented periodically generate periodic responses of the brain. Following a transformation into the frequency domain, the brain's response is often evident at the frequency of stimulation, F, and its higher harmonics (2F, 3F, etc.). This approach is increasingly used in neuroscience, as it affords objective measures to characterize brain function. However, whether these specific harmonic frequency responses should be combined for analysis, and if so, how, remains an outstanding issue. In most studies, higher harmonic responses have not been described or were described only individually; in other studies, harmonics have been combined with various approaches, e.g., averaging and root mean squared summation. A rationale for these approaches in the context of frequency-based analysis principles, and understanding of how they relate to the brain's response amplitudes in the time domain, has been missing. Here, with these elements addressed, the summation of (baseline-corrected) harmonic amplitude is recommended.

Introduction

Frequency-tagging

It has long been known that a stimulus presented at a periodic rate elicits a response from an observer's brain at exactly that rate. For example, a light flickering on and off at a periodic rate, 14 times a second, elicits a measurable response in the electroencephalogram (EEG) of a human observer 14 times a second (Adrian & Mathews, 1934). In the time domain, a response is evident as periodic changes in the brain's response amplitude across time. Following Fourier transformation into a *frequency domain* representation (Fourier, 1822; Danielson & Lanczos, 1942), the response is evident as a high amplitude "peak" at exactly the fundamental stimulus presentation rate (frequency = F), and/or its higher harmonics, i.e., at frequencies that are integer multiples of F (2F, 3F, etc.; Regan, 1966; 1989).

The approach of presenting stimuli and analyzing neural responses at the frequency of stimulation is referred to by many names: "frequency tagging" (Tononi et al., 1998; Srinivasan et al., 1999) is the one that will be used here. Other names for this approach differ mainly on their point of reference: to the responses that appear consistently periodic to stimuli presented at high rates, i.e., "steady-state" responses, e.g., "steady state visual-evoked potentials" (SSVEPs; Regan, 1966; 1989; Di Russo et al., 2002; Heinrich, 2010; Norcia et al., 2015) and "auditory steady state potentials/responses" (ASSRs; Geisler, 1960; Watkin, 2008) or "travelling wave" responses (Engel, Glover & Wandell, 1997); to the stimulation mode itself ("fast periodic visual stimulation" (FPVS); Rossion, 2014; Rossion, Retter & Liu-Shuang, 2020); or the analysis occurring in the frequency domain ("Fourier analysis/synthesis"; Movshon, Thompson & Tolhurst, 1978; Bach & Meigen, 1999; Zhou et al., 2016; or simply "frequency(-domain) analysis", e.g., as in McKeefry et al., 1996). Despite the varying terminologies, the principles of the approach are the same. In a similar vein, various types of stimulation modalities (visual, auditory, somatosensory, cross-modal) and recording methods (electroencephalogram, electroretinogram, functional magnetic resonance imaging, single cell recordings, etc.) may be applied with various participant groups (human adults, children, infants, non-human primates, cats, rodents, frogs, insects, etc.), resulting in some practical differences, but the same fundamentals, of the approach.

In (cognitive) neuroscience research, the frequency-tagging approach is associated with undeniable advantages. As noted early on, this approach is well-suited for specifically relating

brain processes to external events ("This gives a method of tracing the visual messages in the brain, for by means of the flicker rhythm they can be made easy to recognize," Adrian, 1944, p. 361). More recently, its objectivity and sensitivity (i.e., high signal-to-noise ratio, SNR) have been highlighted, and the use of the paradigm is undoubtedly on the rise, having been extended from the study of basic sensory processes, and their modulation by spatial/selective attention, to the direct measurement of higher levels of cognition in recent years (Norcia et al., 2015, for review). However, frequency tagging is still fundamentally limited by outstanding conceptual and methodological ambiguities in dealing with responses occurring across harmonics.

Higher harmonics

Another way of describing frequency tagging is the following: given a periodic stimulus, responses of the brain periodic to that stimulus are investigated. In this formulation, it is evident that the brain's responses may occur at the rate of stimulation, F, but also at the other rates periodic to the stimulation: the higher harmonics (2F, 3F, etc.). For example, a stimulus modulated 8 times a second, at 8 Hz, may generate responses that are evident as amplitude peaks in the frequency domain representation of the brain recording at 8 Hz (F, the first harmonic corresponding to the fundamental frequency¹), but also at 16 Hz (2F, the second harmonic), and 24 Hz (3F, the third harmonic). Since only responses at higher harmonics are periodic to the fundamental frequency, it is uniquely at the higher harmonics, rather than at a diffuse band, that higher frequency constituents of frequency-tagged brain responses are present.

While responses of the brain are not always generated at the higher harmonics, they often do occur (Regan, 1966; Bach & Meigen, 1999; Heinrich, 2010; Vialatte, 2010; Rossion, 2014; Norcia et al., 2015; Zhou et al., 2016; Rossion, Retter & Liu-Shuang, 2020). Note that responses are not always generated at *F*, either; for a classic example, in the case of alternating symmetrical stimulus inputs (e.g., pattern-reversing checkerboards), the brain responds only at 2*F* and higher even harmonics (Cobb, Morton & Ettlinger, 1967; reviewed in Norcia et al., 2015; for different examples: Movshon, Thompson & Tolhurst, 1978; Heinrich, 2010; Zhou et al., 2016). Further, note that throughout this manuscript, only harmonics that are *specific* to their fundamental frequency are addressed, which is always the case when a single stimulus presentation frequency

¹ A note on nomenclature: here, the "first" harmonic is the fundamental stimulation frequency. In another existent convention, the "first" harmonic is the double of the fundamental stimulation frequency.

is used (but for an extension to other cases, with more complex stimulation paradigms, please see the future subsection: *Which harmonics to consider?*).

At present, while higher harmonic responses are an integral part of brain responses, they are not systematically addressed in frequency-tagging research. In many studies, higher harmonic responses are not even reported (e.g., Regan & Regan, 1988; Morgan, Hansen & Hillyard, 1996; Peterzell & Norcia, 1997; Müller, Teder & Hillyard, 1997; Tononi et al., 1998; Heinrich & Bach, 2001; Chen et al., 2003; Braddick et al., 2005; Müller et al., 2006; Di Russo et al., 2007; Wattam-Bell et al., 2010; Cottereau et al. 2011; Kus et al., 213; Coia et al., 2014; Paulk et al., 2015; Min et al., 2016; Bekhtereva et al., 2018; or are extirpated by narrow (band-pass, Gabor, etc.) filtering: e.g., Regan, 1975; Anderson & Müller, 2010; Miskociv & Keil, 2013; Davidson et al., 2020). Does it matter? Yes, at least when there is considerable amplitude at the higher harmonics, relative to *F*. In this case, higher harmonics do contribute significantly to the response measurement: for a dramatic illustration to this effect, see **Fig. 1**.

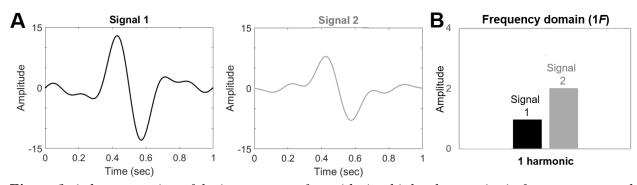


Figure 1. A demonstration of the importance of considering higher harmonics in frequency-tagged response analyses. A) Two synthetic periodic signals, each comprised of five harmonic frequencies. B) In the frequency domain, a consideration of only one harmonic (at the fundamental frequency) describes signal 2 as larger than signal 1. This description is not in agreement with typical time domain response analyses, e.g., peak amplitudes, to compare these signals. Note that this figure will be revisited (expanded) in the penultimate section, Interpreting harmonics.

How often is there considerable amplitude at the higher harmonics? Can the cost of omitting higher harmonics in published studies be evaluated? Unfortunately, most studies do not report whether or not there were responses at higher harmonics, as mentioned above. Moreover, when higher harmonic responses were reported to be present, they were often not described (e.g., "Peaks were also present at the harmonics of the stimulus frequency but were not analyzed in this study," Srinivasan et al, 1999, p.5438; "Higher harmonics may play a role, especially at

lower temporal frequencies (see, for example, the double peaks in the 12-Hz data in Fig. 1), but these are not considered here," Kremers et al., 2010, p. 579; "Note however that 2 Hz is a harmonic of 1 Hz and may actually be a relevant spectral region to consider (albeit outside the scope of this report)," Kosem, Gramfort & van Wassenhove, 2014, Fig. S2; evident in figures but not discussed or included in analyses: Müller et al., 1998; Kaspar et al., 2001; Pastor et al., 2002; 2003; Katzner et al., 2009; Honnegger et al., 2011; Winawer et al., 2013; Chadnova et al., 2018; Eidelman-Rothman et al., 2019; Schettino et al., 2020), preventing a wide-scale review.

From some studies that have described the presence or absence of higher harmonics, there appear to be a couple, specific cases in which their amplitude was *not* considerable, and may be neglected with little cost. The most well-documented case is that in which high stimulus presentation rates are used (as will be demonstrated in the following section; with electrophysiology: Van der Tweel & Verduyn Lunel, 1965; Regan, 1989; Kremers & Scholl, 2001; Luck, 2005; Vialatte et al., 2009; Ross et al., 2000; Capilla et al., 2011; Tlumak et al., 2011; Alonso-Prieto et al., 2013; Heinrich, Groten & Bach, 2015; Retter & Rossion, 2016; with neuroimaging: Puce et al., 1995; Gao, Gentile & Rossion, 2018; Retter, Webster & Jiang, 2019). However, the case of high stimulus presentation rates cannot be readily identified across studies. This is because "high" is dependent on the relationship of the stimulus presentation rate to the duration of the brain responses being measured, by the recording technique, in the assessed population (Keysers & Perrett, 2002; Retter et al., 2020; see also Heinrich, 2010).

A second case is that in which low-amplitude first harmonic responses were reported, such as responses elicited with subtle stimuli (e.g., with no higher harmonic amplitude above noise: Brazier, 1964; Retter & Rossion, 2017; Park, 2018; Lochy, Schiltz & Rossion, 2020; with very low higher harmonic amplitudes: Ales et al., 2012; Moungou, Thonnard & Mouraux, 2016; McFadden et al., 2014). However, this case also does not allow general inferences: low first harmonic amplitudes may still coincide with large higher harmonic amplitudes (see the upcoming section, *Frequency-tagged responses in the frequency domain*; also, e.g., Vialatte et al., 2009; Capilla et al., 2011; Alonso-Prieto et al., 2013; Gaume, Vialatte & Dreyfus, 2014), such that the amplitude of the first harmonic itself is not diagnostic.

On the other hand, considerable amplitude at higher harmonics has been reported in a wide array of studies. For example, higher harmonics often *exceed* the fundamental in studies on the brain's responses for an extensive range of processes (with *F* usually below 8 Hz, recorded to

visual stimuli with EEG/MEG): from luminance (patterns: Davilda, Srebo & Ghaleb, 1998; Vialatte et al., 2009; Capilla et al., 2011; Gaume, Vialatte & Dreyfus, 2014; electrocorticography: Winawer et al., 2013; electroretinogram: Baker & Hess, 1984), to color and motion (Tyler & Kaitz, 1977; McKeefry et al., 1996), to face perception (Alonso-Prieto et al., 2013; Liu-Shuang, Norcia & Rossion, 2014); below about 40 Hz to auditory stimuli: Ross et al., 2000; see also Tlumak et al., 2011). Higher harmonics may also be present, each with a lower amplitude than the fundamental, but with their amplitude distributed across a large range of harmonic frequencies (e.g., Vialatte et al., 2009; Capilla et al., 2011; Alonso-Prieto et al., 2013; Gaume, Vialatte & Dreyfus, 2014; Painter et al., 2014; Retter & Rossion, 2016; Cunningham, Baker & Pierce, 2017). Considerable higher harmonics have also been demonstrated with low-temporal resolution techniques, including fMRI, given appropriately slow stimulus presentation frequencies (e.g., with *F* well below 0.1 Hz; motor activity: Bandettini et al., 1993; luminance patterns: Engel, Glover & Wandell, 1997).

In some cases, the conclusions of studies considering and not considering higher harmonics can be compared. For example, in frequency tuning studies, without considering higher harmonics, maximal visual responses were reported to stimuli modulated at about 10-15 Hz with EEG (e.g., Regan, 1966; Pastor et al., 2003; Ding, Sperling & Srinivasan, 2006; see also Vialatte et al., 2009). However, when higher harmonics were considered, the lowest stimulation frequency tested (3 Hz) yielded the maximal visual EEG responses, being over three times higher than the responses to 12 Hz stimulation with natural images (Retter et al., 2020; Fig. S3). Similarly, maximal auditory responses were reported to stimuli modulated at about 40 Hz with EEG (e.g., Galambos, Makeig & Talmachoff, 1981; Ross et al., 2000; Pastor et al., 2002), but a consideration of higher harmonics produced the maximal auditory EEG responses at the lowest stimulation frequency tested (0.75 Hz; Tlumak et al., 2011; Fig. 4). Overall, while it is thus impossible to ascertain what the impact of unreported, or uncharacterized, higher harmonic responses in most studies may have been, it is likely that it was often considerable.

Should higher harmonic responses be combined, and if so, how?

At present, harmonics are surrounded by many questions: why do they occur? What do they represent? Which, or how many, harmonics should be considered? Should they be taken into account for response identification and measurement, and if so, how? Indeed, the lack of

understanding and standard practice regarding higher harmonics has limited the ease (i.e., objectivity) of frequency-tagged response identification and measurement. This is particularly significant because objectivity is given as a primary advantage of the frequency tagging technique, contributing to its increasing application in (cognitive) neuroscience research and clinical applications (e.g., see Norcia et al., 2015; Rossion, Retter & Liu-Shuang, 2020).

In previous studies that reported harmonic responses, most often these responses have been described individually, e.g., at *F*, 2*F*, 3*F*, etc., and have not been taken into account for response measurement (e.g., Tyler & Kaitz, 1977; Bandettini et al., 1993; Srinivasan et al, 1999; Herrmann, 2001; Vialatte et al., 2009; Ross et al., 2000; Capilla et al., 2011; Rossion & Boremanse, 2011; Ales et al., 2012; Alonso-Prieto et al., 2013; Painter et al., 2014; Moungou, Thonnard & Mouraux, 2016; Cunningham, Baker & Pierce, 2017). While considering harmonic responses separately is considerably better than not at all, individual harmonic responses do not represent independent aspects of a time-domain response (e.g., see Tang & Norcia, 1995; for dependent harmonic amplitude examples: Retter & Rossion, 2016; Zhou et al., 2016; for qualitatively similar neighboring harmonic examples: Rossion, 2014; Jacques, Retter & Rossion, 2016; Rossion, Retter & Liu-Shuang, 2020; Zemon & Gordon, 2018; see the penultimate section, *Interpreting Harmonics*).

In practice, considering higher harmonic responses improves response detection, measurement and classification (e.g., Davilda, Srebo & Ghaleb, 1998; Cebulla, Stürzebecher & Elberling, 2006; Tlumak et al., 2011; Retter & Rossion, 2016; Zemon & Gordon, 2018; for brain-computer/machine interfaces: Muller-Putz et al., 2005; Chen et al., 2015; Cetin, Ozekes & Varol, 2020). Combining harmonics is particularly useful for comparing response amplitudes across experimental conditions. Otherwise, if one input produces a response with larger amplitudes than another input at some harmonics but not others, how could these responses be evaluated overall? Or, how could the relative change (e.g., percent increase) of one response relative to another be calculated overall? In some previous studies, harmonic responses have been combined with various approaches, such as root mean squared summation (i.e., the square root of the summed squared amplitudes, also known as the "root sum square", or "summation in quadrature"; e.g., Hou et al., 2003; Appelbaum et al., 2006; 2010; Tlumak et al., 2011), (weighted) summation (e.g., Cheng et al., 2002; Wang et al., 2008; Zhang et al., 2011), or averaging (e.g., Liu-Shuang, Norcia & Rossion, 2014; Lochy, Van Belle & Rossion, 2015;

Milton et al., 2020). However, these approaches have not been justified, and have not been related to approaches analyzing the brain's response amplitudes in the time domain (or physiologically: see Heinrich, 2010).

In the following, a validated methodology for combining (baseline-corrected) harmonic amplitudes through simple summation will be provided. This approach derives from a theoretical basis of how signals over time are represented through mathematical transformations into the frequency domain (second section: Frequency-domain representations), extended to experimental responses in practice (third section: Frequency-tagged responses in the frequency domain). This approach was indicated empirically by Retter and Rossion (2016), and it has since been applied in a number of studies, however, primarily by those authors or associated research groups (e.g., Xu et al., 2017; Beck, Rossion & Samson, 2018; De Keyser et al., 2018; Leleu et al., 2018; Chemin et al., 2018; Guillaume et al., 2018; Gwinn et al., 2018; Gwinn & Jiang, 2019; Dwyer, Xu & Tanaka, 2019; Van der Donck et al., 2019; Damon et al., 2020; Fisher et al., 2020; van de Walle de Ghelcke et al., 2020). To be of further use to the scientific community, the approach requires deeper methodological evaluation and, especially, evaluation in a theoretical context, which is the goal throughout the present manuscript. From this, some practical guidelines are offered (fourth section: Combining harmonic responses) and implications are drawn for the interpretation of harmonic responses more generally (fifth section: *Interpreting* harmonics).

Frequency-domain representations

Sine waves

When a signal is transformed into the frequency domain (by means of a Fourier transform), it becomes represented through a combination of sine waves, which are the fundamental units of the frequency domain. While there are many texts on the mathematics of frequency transformations and representations (e.g., Press, Falnnery & Teukolsky, 1993; Smith, 1997; Strang, 2007; Patel, 2012; Forinash & Christian, 2016; Gonzalez & Woods, 2018), a basic understanding of sine waves and their combination is a sufficient foundation for the interpretation of multi-harmonic responses of the brain (Regan, 1989).

Briefly, sine waves are trigonometric functions that describe periodic signals in terms of frequency, amplitude, and phase (**Fig. 2**). The *frequency* of a sine wave describes the number of

cycles (of 360°; equivalent to 2π radians) per unit of time or space (time is typically given in units of cycles/sec = \sec^{-1} = Hertz = Hz). Note that the cycles of sine waves are periodic, and could repeat their pattern infinitely, as a circle could be endlessly traced (the sine wave, as in **Fig. 2B**, derives from the y-axis values of a unit circle, as shown in **Fig. 2A**). The *amplitude* of a sine wave is defined along the y-axis (e.g., in **Fig. 2B**, the sine wave, spanning from -1 to 1, has an amplitude of 1; its unit in EEG recordings is typically microvolts = μ V). The *phase* of a sine wave is a measure of its starting angle (indicated by *theta* in **Fig. 2A**), with an arbitrary beginning at zero (in units of degrees (deg; °) or radians (rad)), as is shown in **Fig. 2B**. Changes in frequency, amplitude, and phase, that help demonstrate these properties, are illustrated in **Fig. 2C**. For those whom it helps to see it mathematically, the expression of a sine wave, as a function of x, is: $y(x) = a\sin(2\pi fx + \phi)$, where a = amplitude (scaling on the y-axis); f = frequency (by cycles); and $\phi = \text{phase}$ (x-axis shifts).

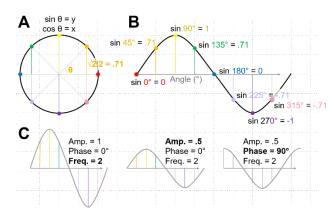


Figure 2. The sine wave. A) A unit circle, with a radius of 1, illustrates the underlying trigonometry of sine (and cosine) functions. B) A sine wave derives from the y-axis values of points on the unit circle as a function of angle (here, this is emphasized with corresponding angle colors). A complete cycle of a sine wave contains 360°. (Note that a cosine wave, which derives from the x-axis values, has the same shape but with a 90° phase shift.) C) Sine waves

are described in terms of: frequency (cycles per unit); amplitude (y-axis scale); and phase (x-axis shift). The given examples exhibit sequential changes in these properties (beginning in reference to Panel B, then from left to right; the changed property is indicated in bold). **Key**) Amp. = Amplitude; Freq. = Frequency.

A lot of sine waves

A frequency-domain representation of a signal is essentially a lot of sine waves. That is, when a signal is transformed into the frequency domain, the resultant x-axis describes the frequency of its constituent sine waves. The other descriptors of sine waves, amplitude and phase, are described in the transformed, complex-valued y-axis at each frequency, which is typically plotted

as separate amplitude and/or phase frequency spectra². The resolution (x-axis sampling) of the frequency-domain spectrum is the inverse of the signal recording length, and the range spans from 0 to half of the signal sampling rate (note that these properties have practical implications for frequency tagging experimental design, e.g., as addressed in Bach & Meigen, 1999). The *combination*, through summation, of these sine waves described in the frequency domain reconstructs the original signal in the time domain. Here, the focus will be on periodic signals over time, but note that frequency-domain analyses can be applied in many settings, e.g., signals over space or over two dimensions.

In the simplest case, a periodic signal that is a perfect sine wave is represented in the frequency domain by a single frequency, representing a single sine wave (**Fig. 3A**). Another way to understand this is to observe that in this case the frequency, amplitude, and phase of a single sine wave in the frequency domain are sufficient to reconstruct the original signal in the time domain. In most cases, signals are more complex (i.e., non-sinusoidal), but this does not pose a problem: a *combination* of sine waves at different frequencies can *sum* to model any signal. In a classic example, a periodic squarewave signal is shown to be represented with a sum of sine waves specific to its periodicity (**Fig. 3B**). Non-periodic signals, e.g., event-related potentials (ERPs) to temporally jittered stimuli can also be represented in the frequency domain, but since they are not specific to limited frequencies, their interpretation does not correspond to that of frequency-tagged signals (**Fig. 3C**). Although frequency-based analyses of non-periodic signals may be applied (e.g., see Regan, 1989; Basar & Shurmann, 1994; Herrmann et al., 2014; see also Chemin et al., 2018), these are outside the present focus on frequency tagging.

It may be observed that a simple sine wave ranging from -1 to 1 in the time domain has an amplitude of 1 in the frequency domain, but that the relationship between the time-domain and frequency-domain amplitudes for multi-harmonic signals is more complex (compare **Figs. 3A** and **3B**). However, there is a direct relationship between these dimensions: because energy is

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² Note that in frequency-domain transformations, technically a complex-valued combination of sine waves and cosine waves is used to represent the signal. In many discrete, fast Fourier transforms, the sine component carries only the amplitude information and the cosine component carries only the phase information. Here, "sine waves" are referred to as complex entities themselves, combining both amplitude and phase information. Additionally, note that phase spectra are rarely plotted in the same format as amplitude spectra, because: 1) their values are circular, e.g., with equivalent distance from 0-359° and 0-1°; see an alternative plotting example in **Fig. 6D**; and 2) the phase at non-frequency-tagged signal frequencies is random, i.e., full-range noise.

conserved from the time to frequency domain, the sum of the squared amplitudes of the time-domain signal equals the sum of the squared root-mean-square amplitudes of the frequency-domain signal (Parseval's relation; Parseval des Chênes, 1806; e.g., see Smith, 1997)³. For example, the sum of the squared amplitudes per cycle of the time-domain signal in **Fig. 3A** is equal to 0.5, and the sum of the squared root-mean-squared amplitudes of its discrete frequency-domain signal is equal to 0.5. Multi-harmonic signals also preserve this relationship, although their time-domain amplitude range does not directly relate to their frequency-domain amplitude (being affected by phase; see the fourth-section subsection: *What about phase?*).

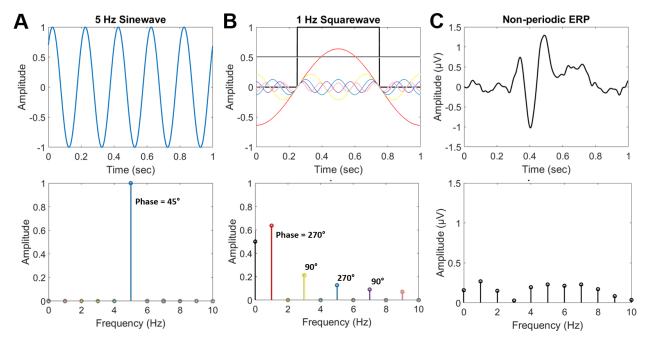


Figure 3. Lots of sine waves build frequency-domain representations of signals. Upper row: time-domain signals. Lower row: these signals transformed into the frequency domain. A) A periodic sine wave is represented with a single frequency in the frequency domain. B) A periodic squarewave (thick, black line) is represented with a combination of many, specific harmonic frequencies (lines colored correspondingly across top and bottom panels). Literally, the sum of these (and higher, not illustrated) colored lines' amplitude at each time point reconstructs the original signal. C) A non-periodic, event-related potential (ERP) signal is represented with a combination of many nonspecific frequencies (data from Retter et al., 2020). Note several properties of the frequency-domain signal: 1) the 0 frequency bin reflects the mean amplitude (DC offset) of the signal; 2) the x-axis resolution is the inverse of the signal recording duration; 3)

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³ In the time domain, energy is equal to power over time, which is equal to the sum of the squared amplitudes. In the frequency domain, energy is equal to the sum of the squared root-mean-square amplitudes (root-mean-square amplitude of a sine wave = amplitude/ $\sqrt{2}$; see Smith, 1997).

although the frequency domain is plotted only until 10 Hz here, its range spans further (up to half of the signal sampling rate); and 4) although only the phase of tagged frequencies is indicated on the lower row here, each frequency in the spectrum has a corresponding phase value.

Frequency-tagged responses in the frequency domain

One harmonic; a lot of harmonics

Frequency tagging is an approach in which stimuli are presented *periodically* in order to generate *periodic* responses of the brain, that can thus be identified in the frequency domain at specific frequencies harmonic to the stimulation, i.e., the fundamental and the higher harmonic frequencies. In the following, examples will be taken only for harmonics that are specific to a single tagged frequency: again, for determining specific harmonics in the context of multiple tagged frequencies, see the fourth-section subsection: *Which harmonics to consider?*).

According to the principles of frequency analyses, a simple, sinusoidal brain response would be represented only at the fundamental frequency F, while more complex brain responses would be represented with a combination of F and its higher harmonics, 2F, 3F, etc. Generally, this is evidenced with experimental brain responses. In the event that the brain responses are nearly sinusoidal, the response is dominated by amplitude at F (e.g., at a high stimulus presentation rate: **Fig. 4A**); in the event that the responses of the brain are complex, a combination of sine waves at different frequencies (i.e., the higher harmonics) can sum to model any signal (**Fig. 4C**). In many studies, complex, non-sinusoidal responses of the brain evoked over time are represented in the frequency-domain not only at F, but with considerable amplitude at its higher harmonics (as addressed in the *Introduction*, e.g., Brazier, 1964; Van der Tweel & Verduyn Lunel, 1965; Regan,1966; 1989; Donker, 1975; Sieving et al., 1998; Bach & Meigen, 1999; Ross et al., 2000; Kremers & Scholl, 2001; Vialatte et al., 2009; Heinrich, 2010; Vialatte, 2010; Tlumak et al., 2011; Alonso-Prieto et al., 2013; Norcia et al., 2015; Retter & Rossion, 2016; Zhou et al., 2016; Rossion, Retter & Liu-Shuang, 2020).

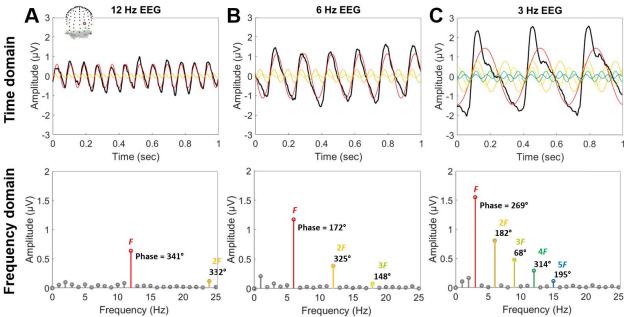


Figure 4. The higher the stimulus presentation rate (F), generally the lower the amplitude of higher harmonic responses, (2F, 3F, etc.), relative to the fundamental, F. Upper row: example brain responses, recorded with EEG (channel POO6 displayed here), were elicited from periodic visual stimulation of natural object images at various presentation frequencies (thick black lines; data from Retter et al., 2020). Harmonic sine waves from the frequency-domain analysis, as represented below, are superimposed in color, to illustrate their relationship with the original signal. Lower row: Frequency-domain representations of these signals. The amplitude of harmonic responses above 5% of that of the fundamental are plotted in color, corresponding with the upper row. A) 12 Hz stimulation elicits nearly sinusoidal brain responses. B) Intermediate, 6 Hz stimulation. C) 3 Hz stimulation elicits more complex brain responses in the time domain, represented with frequency-domain amplitude more distributed across higher harmonics.

Indeed, higher harmonic responses may be accounted for in relation to the complex (i.e., non-sinusoidal) responses of the brain, in accordance with the principles of frequency-domain analysis of periodic signals (as in Regan, 1989; Heinrich, 2010; Zhou et al., 2016; Norcia et al., 2015; Rossion, Retter & Liu-Shuang, 2020). This account explains that higher harmonics are present when complex brain responses are present, but does not implicate a specific source of complex brain responses (see Heinrich, 2010). However, it is important to note that complex brain responses are not a product of frequency tagging, and may equivalently occur with non-periodic (event-related) stimulus-presentation modes⁴.

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⁴ Although largely beyond the scope here, note that it is extensively debated whether frequency-tagged EEG responses reflect the (linear) super-position of event-related potentials (ERPs), or whether they reflect an interaction with endogenous oscillations in the brain (see Donker, 1975; Galambos, Makeig & Talmachoff, 1981; Herrmann, 2001; Makeig et al., 2002; Heinrich, 2010; Capilla et al., 2011; Gruss et al., 2012; Keitel,

The harmonics do not represent new information, specific to the frequency-domain: they are merely highlighted in an alternative, frequency-domain representation of the original time-domain signal (certain variations may be represented more or less clearly in each domain). These domains are interchangeable: as time-domain data can be transformed into the frequency domain, frequency-domain data can also be inversely transformed back into the time domain; indeed, time-domain responses can be reconstructed from frequency-domain harmonic amplitudes and phases (e.g., Sieving et al., 1998; Ruhnau et al., 2016). The next section focuses on the combination of harmonic responses; however, individual harmonics will be further addressed in the penultimate section, *Interpreting Harmonics*.

Imperfect signals: accounting for baseline noise

In theoretical examples of signal transformation into the frequency domain (as in the preceding section, *Frequency domain representations*), the signal is pure signal. In frequency-tagging, as in all brain recordings, the signal (here, i.e., the responses of the brain at the tagged frequencies), also carries "noise", a term that refers to both non-event-related brain activity and artifacts (e.g., Regan, 1989; Luck, 2005). Note that there are many methods for correcting for noise, i.e., isolating signal, in frequency-tagging research, although a discussion of these is more general than the scope of this manuscript (see instead, e.g., Meigen & Bach, 2000; Appendix 2 of Norcia et al., 2015). In the examples given here, a simple correction for noise will be applied that subtracts a local baseline from the amplitude of the frequencies of interest (e.g., Retter & Rossion, 2016) ⁵. The baseline is defined as the mean amplitude of a symmetrical range of neighboring (i.e., continuously adjacent⁶) frequency bins (for theoretical justification, see Regan, 1989; Norcia et al., 2015; e.g., Peterzell & Norcia, 1997; Meigen & Bach, 2000; Boremanse, Norcia & Rossion, 2013; with power rather than amplitude: Srinivasan et al., 1999; Vialatte et

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Quigley & Ruhnau, 2014; Heinrich, Groten & Bach, 2015; Norcia et al., 2015; Retter & Rossion, 2016; Zoefel, Oever & Sack, 2018).

⁵ Note that, further, the signal and noise may interact non-linearly (supra-additively), but when the signal is much (e.g., three or four times) greater than noise, this modest contribution is negligible (Strasburger, 1987; Peli, McCormack & Sokol, 1988; Norcia et al., 1989; see Bach & Meigen, 1999). Particularly for weaker signals, a more conservative baseline correction could be computed as the square root of the signal-power-minus-noise-power: see Appendix 1 of Norcia et al., 1989.

⁶ Please note an exception: sometimes the first adjacent bin, on either side of the frequency bin of interest, is excluded, so as to avoid overspill, i.e., signal leakage, in the noise estimate at high frequency resolutions (e.g., Rossion et al., 2012).

al., 2009; Mouraux et al. 2011). This method is used to provide a measure of signal amplitude in the frequency domain that is relatable (i.e., both in the same unit) to amplitude in the time domain, and with a noise level at zero, while compensating for local variations of noise inherent to brain recordings across the frequency spectrum.

Combining harmonic responses

Combining harmonic response amplitude

The combination of sine waves is simple: sine waves sum linearly to reconstruct a signal. However, with the goal of identifying and measuring overall response amplitude in the frequency domain, since sine waves carry both amplitude and phase information, their sum is not intuitive to interpret in terms of amplitude only (or phase only). (Note that there are alternative approaches for combining harmonics that incorporate both amplitude and phase, however these approaches make use of phase as an indicator of reliability (coherence), typically across short stimulation durations (e.g., Jervis et al., 1983; Strasburger, 1987; Delorme & Makeig, 2004).) Further, while the amplitude of a single sine wave in the frequency domain directly relates to its time-domain peak amplitude, i.e., half its positive to negative peak range (e.g., Fig. 3A; similarly, see Fig. 4A), the frequency-domain amplitude of complex time domain signals (summed sine waves) is not as easily visualized from the time domain. Perhaps for these reasons, various approaches have been taken for the combination of frequency-tagged multi-harmonic brain response amplitude in the frequency domain (e.g., as mentioned previously, averaging or root mean squared summing, e.g., respectively, Liu-Shuang, Norcia & Rossion, 2014; Hou et al., 2003).

The **summation of harmonic amplitudes** is recommended here for identifying and measuring the overall brain response (based on Retter & Rossion, 2016; see also Heinrich, 2009). In the study of Retter & Rossion (2016), this approach was validated empirically, by qualitative comparison of time and frequency domain responses, in the situation where several equivalent time-domain EEG responses were produced by several slow target stimulus presentation frequencies. There, it was observed that despite different distributions of harmonic amplitudes stemming from the different fundamental target stimulus presentation frequencies (1.1 to 2.5 Hz), the summation of baseline-subtracted harmonic amplitude across a common frequency range led to equivalent overall amplitudes, that related to approximately equivalent

response amplitude peaks in the time domain by visual inspection (see **Fig. 5A&B**, row 1, here, for examples of reprocessing of that data in combination with the underlying harmonic distributions). Moreover, a faster stimulus presentation rate (4.2 Hz), which produced visually lower amplitude deflections in the time domain (**Fig. 5C**, row 1), also produced a lower summed-harmonic response amplitude.

Here, these data are revisited quantitatively, with typical time-domain interpretations of response amplitudes: peak-to-peak amplitude of the largest deflections, and the area under the curve of the response deflections (**Fig. 5**, row 4). Note that an exact comparison of specific deflections, as is more commonly done in relating brain responses, is possible for the conditions at 1.1 and 1.4 Hz, but that a different response pattern is observed for the condition at 4.2 Hz, preventing such a direct comparison.

The summed-harmonic response amplitude is shown to be congruent with these measures (**Fig. 5D**). Critically, other approaches for harmonic combination would not have led to these conclusions when comparing conditions. Here, in the frequency domain, a large fundamental harmonic amplitude relates to a smaller number of harmonic responses (with an amplitude above $0.1~\mu\text{V}$). Therefore, for example, averaging the harmonic responses would have generated lower amplitude responses the slower the stimulus presentation frequency (1.1 Hz < 1.4 Hz < 4.2 Hz; **Fig 5D**). For another example, the root-mean-squared harmonic amplitude would have generated the highest amplitude for the highest stimulus presentation rate (4.2 Hz; **Fig 5D**). For a last example, using non-baseline-corrected amplitudes would have produced a larger response at 1.1 Hz than 1.4 Hz, since "noise" would have been included at more, and lower-frequency (noisier), harmonics at 1.1 Hz.

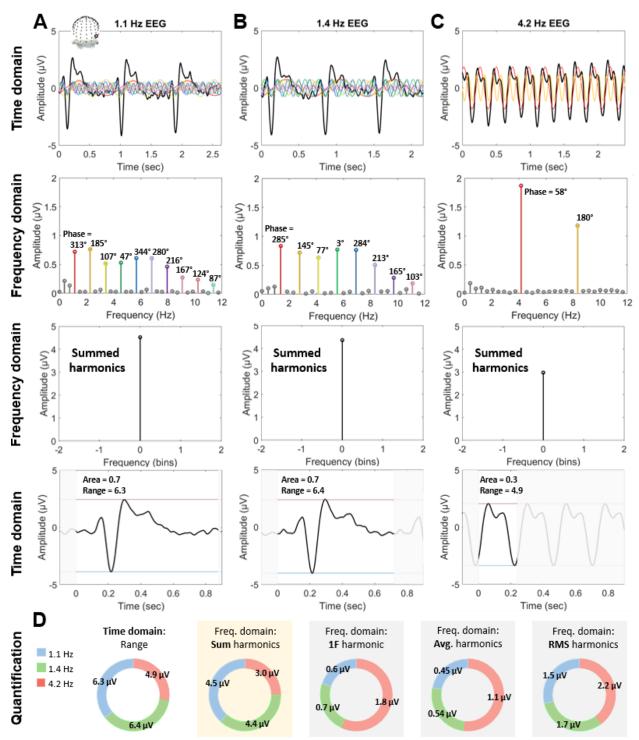


Figure 5. The combination of harmonic amplitude. For A-C: Row 1: example brain responses, recorded with EEG (channel PO10 displayed here), were elicited from periodic visual stimulation of natural face (vs. object) images at various frequencies (data from Retter & Rossion, 2016). Row 2: Frequency-domain representations of these responses. The amplitude of harmonic responses above 0.1 μ V are plotted in color, and these harmonic sine waves are superimposed in the corresponding color in Row 1. Row 3: The colored harmonic responses above are summed (set at

bin 0), following a baseline subtraction of "noise", defined as the average amplitude of the two adjacent frequency bins. Row 4: Similar response amplitudes are demonstrated in the time domain in Panels A and B, consistent with Row 3. Time outside of one cycle duration is shadowed in gray, and the response amplitude range is emphasized between the horizontal red and blue lines. A) 1.1 Hz target (face) stimulation elicits complex brain responses. B) 1.4 Hz target stimulation elicits a similar response to 1.1 Hz stimulation in the time domain and the amplitude of summed, baseline-subtracted harmonics in the frequency domain, despite a different distribution of harmonic frequency amplitudes. C) 4.2 Hz target stimulation elicits more simple and lower amplitude neural responses in both the time and frequency domains. D) Quantification in the time domain (amplitude range) is compared with different methods of harmonic assessment in the frequency domain, with baseline-subtracted amplitudes. The sum of harmonics provides a better correspondence with the time domain, across conditions, than the fundamental harmonic (F) only, average of harmonics, or root-mean-square (RMS) of harmonics.

Thus, summing baseline-subtracted harmonic amplitudes is advantageous for a correspondence with interpretations of time-domain brain responses. This approach has been used to quantify and compare overall response amplitude in a number of studies following Retter & Rossion (2016) as mentioned previously (e.g., including time-domain correspondences: De Keyser et al., 2018; Leleu et al., 2018; frequency-domain analyses only: Xu et al., 2017; Beck, Rossion & Samson, 2018; Chemin et al., 2018; Guillame et al., 2018; Gwinn et al., 2018; Gwinn & Jiang, 2019; Dwyer, Xu & Tanaka, 2019; Damon et al., 2020)⁷.

If measures other than amplitude are desired, e.g., signal-to-noise ratio, z-scores, or another statistic, the harmonic amplitudes can be extracted with an inclusion of a baseline frequency range (i.e., as a "chunk" of X Hz, centered around each frequency-of-interest), and then summed *prior* to these baseline-relative computations (Retter & Rossion, 2016; see also appendix 2 of Norcia et al., 2015; Box 2 of Rossion, Retter & Liu-Shuang, 2020). In this way, a single statistical measure can be applied to the combined harmonic amplitude relative to its combined baseline amplitude, i.e., "noise". Note that different approaches for combining harmonics may serve different ends, in that they describe different aspects of the signal, e.g., the root-mean-squared amplitude relates to the equivalent power of a flat (non-sinusoidal) signal, however, these aspects must be justified in relation to their physiological meaning.

⁷ See also publications motivated by the as yet unpublished findings of Retter & Rossion, 2016, from the Face Categorization Lab (https://face-categorization-lab.webnode.com/): Dzhelyova & Rossion, 2014, Dzhelyova & Rossion, 2014b; Jacques, Retter & Rossion, 2016, Jonas et al., 2016, Liu-Shuang, Torfts & Rossion, 2016; Lochy, Van Reybroeck & Rossion, 2016, and Retter & Rossion, 2016b).

What about phase?

As addressed previously, there is a direct relationship between signal amplitude in the time and frequency domains. As a reminder, this relationship is given by Parseval's relation, which states that energy is conserved across the time domain (where energy equals the sum of the squared root-mean-square amplitudes) and frequency domain (where energy equals the sum of the squared root mean amplitudes). In light of this, the amplitude across the harmonics relates to the overall amplitude of the signal in the time domain, regardless of phase.

However, in order to fully relate signals across the time and frequency domains, both the amplitude *and phase* of the representative frequency domain sine waves need to be taken into account. Without phase information, the fluctuation of amplitude across time, e.g., affecting local amplitude peaks, cannot be determined. Therefore, there is a cost towards relating time- and frequency-domain signals when excluding phase information. However, this cost is reasonably minor: for example, as relative phase changes across harmonics, it is possible that the latency of signal peaks varies, but that their amplitude does not (**Fig. 6A&B**). When relative phase does affect peak amplitudes, this influence is limited (e.g., compare **Fig. 6B&C**). Moreover, despite relative phase changes, the area under the curve of the time-domain signal may remain approximately constant (**Fig. 6A-C**; see also Heinrich, 2010)⁸.

Moreover, in frequency tagging, it is worth remembering that the phase is not arbitrary: the phase of each relevant harmonic is determined relative to the time domain signal. In other words, the aligning positive and negative peaks of the sine waves across harmonic frequencies correspond to the time of the positive and negative peaks of the signal in the time domain (see again **Fig. 3B**, for an example of deconstructive (when the signal = 0) and constructive (when the signal = 1), phase-locked harmonic sine wave superpositioning). This leads to phase differences across harmonics that are similar to describe time-domain signals with similar temporal dynamics, despite the use of different stimulation frequencies (**Fig. 6D**; see also Strasburger, 1987). Thus, the influence of phase on combined harmonics is largely invariant of the stimulus presentation frequency, given consistent temporal dynamics of the response (as hinted at empirically, e.g., Appelbaum, 2006; Retter & Rossion, 2016). Finally, it is worth noting a couple of helpful restrictions in the context of frequency-tagging for combining harmonic responses:

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⁸ In any case, it remains unclear at present how phase could be combined meaningfully across harmonics, beyond time-domain latency, to relate to functional, physiological processes; see Strasburger, 1987.

only one sine wave is represented at each frequency bin, and non-harmonic frequencies are not considered, such that the response is fully periodic at the cycle duration of the fundamental frequency, F.

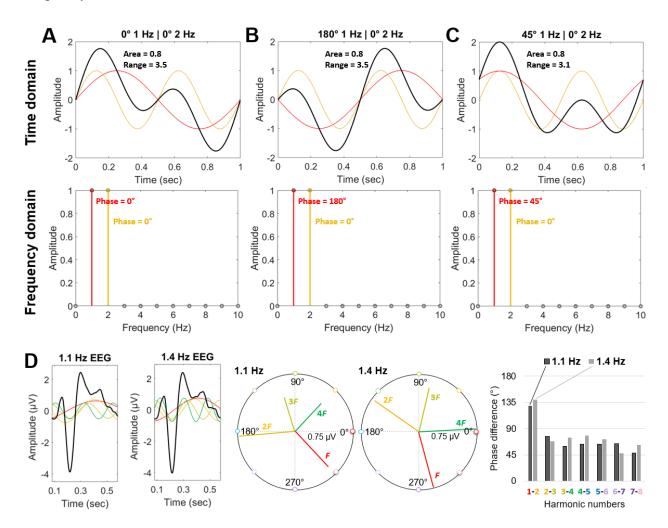


Figure 6. The influence of harmonic phase on the combination of harmonic amplitude. Synthetic time-domain signals (in thick black lines; Row 1) are the sum of two harmonic sine waves: a 1 Hz sine wave with varying phase (A: 0°; B: 180°; C: 45°; plotted in red) and a 2 Hz sine wave with constant phase (0°; plotted in orange). Each sine wave has an amplitude of 1. Row 2: Frequency-domain representations of these signals show the consistent 1 Hz amplitude at 1 and 2 Hz across the Panels. In the time domain, the area under the curve (absolute value) also remains

 9 In frequency-tagging with a single stimulation frequency, there are not multiple sine waves of the same frequency that interfere with each other, e.g., sine waves with a 180° phase difference that produce complete interference (zero amplitude sum). Further, when a complete F cycle is considered, the amplitude is representative of the complete signal (which is not the case for multiple (non-harmonic) frequencies that may sum differentially across short time segments of evaluation). Note that these conditions are not always met in other contexts in which frequency-based analyses are performed.

approximately constant, although the amplitude peaks (positive and negative) and range may be influenced by the relative harmonic phase. **D**) 1.1 Hz and 1.4 Hz EEG responses (data from **Fig.** 5). Left panel: Time-domain responses, highlighting the phase of the first four harmonics. Middle panel: Polar plots, in which each of these four harmonic frequency-domain responses is represented with a vector: angle = phase; length = amplitude. Right panel: Despite the different fundamental frequencies, the difference across sequential harmonics' phase is similar.

Which harmonics to consider?

Before combining harmonics, a decision of which harmonics to consider is required. To this extent, harmonics-of-interest (similarly to a region-of-interest) must be defined. The first criterion for determining harmonics-of-interest is whether a higher harmonic is *specific* to its fundamental frequency. As mentioned previously, in frequency-tagging paradigms using a single stimulation frequency, the higher harmonics are always specific to the fundamental frequency. However, in paradigms deploying multiple stimulation frequencies, unspecific harmonics may occur, which are often excluded from the analyses (for a paradigm-focused review: Norcia et al., 2015). For example, two stimuli may be simultaneously presented at different spatial locations, one at 8 Hz (F_1) and the other at 6 Hz (F_2). If a response occurred at 24 Hz, it would not be specific to either stimulus, being the 3rd harmonic of 8 Hz (3 F_1), and the 4th harmonic of 6 Hz (4 F_2), and would therefore be excluded from the analyses of responses to each stimulus (for further examples: **Table 1**).

A second consideration for determining harmonics-of-interest aims to exclude extreme harmonic frequencies (e.g., the 30th harmonic of 8 Hz, at 240 Hz) at which no signal is expected or found. A limited selection of harmonics has been made based on various types of criteria: 1) amplitude, power, signal-to-noise ratio, or significance thresholds (e.g. Donker, 1975; Hou, Pettet & Norcia, 2008; Rossion et al., 2015); 2) frequency range (e.g., Sieving et al., 1998; Jacques, Retter & Rossion, 2016; Leleu et al., 2018; Zemon & Gordon, 2018); 3) harmonic series number (e.g., Donker, 1975; Appelbaum et al., 2006; Wittevrongel et al., 2018); 4) in relation to other stimulation frequencies (e.g., Heinrich et al., 2009; Milton et al., 2020); and 5) correlation with the time-domain response (e.g., Badettini et al., 1993; Engel, Glover & Wandell, 1997).

The use of a limiting frequency range is recommended here, either as determined *a priori*, or from an assessment of the highest harmonic meeting a threshold (in terms of amplitude, signal-to-noise ratio, or significance). This is recommended because the upper

frequency limit of harmonic responses, although affected by the overall strength of the signal, generally relates to the highest frequency that is strongly represented in the signal (see the penultimate section, *Interpreting harmonics*). The upper frequency limit of harmonic responses is thus often conserved across fundamental stimulation frequencies (see Fig. 2 of Retter & Rossion, 2016).

Note that the highest harmonic-of-interest can be determined either at the group level across conditions, or as presented by any participant for any condition, but that typically a common range of frequencies-of-interest should be used across participants and conditions (e.g., Jacques, Retter & Rossion, 2016). In this approach, there may be harmonic frequencies included for consideration at which there is no signal (e.g., in some participants, conditions, or regions-of-interest); however, including a small number of such frequencies is likely less detrimental (given that an appropriate baseline noise correction is applied, e.g., so that approximately zero amplitude values are added) than missing some frequencies containing a weak signal. Similarly, although responses are typically expected to occur consecutively across harmonic frequencies, in the event that a small number of within-range harmonic frequencies do not contain signal (above threshold), including them is typically tolerable (e.g., Liu-Shuang, Norcia & Rossion, 2014; Rossion, Retter & Liu-Shuang, 2020).

Finally, in some cases harmonic responses appear to be qualitatively different from one another. This may occasionally be related to physiological sources: for example, different harmonic response patterns are generated from the recordings of frequency-tagged responses from single- vs. double-opponent cortical cells (Movshon, Thompson & Tolhurst, 1978). However, more often, physiological sources may only be tentatively inferred, e.g., when different EEG scalp topographies are observed at different harmonic frequency ranges (e.g., Rossion, 2014; see the following-section subsection, *What do higher harmonic responses represent?*). In this case, is it appropriate to select subranges of qualitatively homogeneous harmonics to consider and/or combine? Perhaps, although it should be remembered that harmonic responses are not independent of one another (e.g., Retter & Rossion, 2016; Zhou et al., 2016), and therefore should *also* be described individually and/or summed all together (following-section subsection: *Should higher harmonic responses be combined, and if so, how? (Reprise)*).

It is not advised to select or subgroup harmonics *a priori* in accordance to only their number, unless this is explicitly derived from the stimulation paradigm (see **Table 1**). For example, there is a persistent history of considering the 1st *vs.* 2nd harmonic response (Baker & Hess, 1984; Burns, Elsner & Kreitz, 1992; Falsini et al., 1999; Kremers & Scholl, 2001; Pastor et al., 2007; Saupe et al., 2009; the 1st vs. 2nd harmonic, rather than odd vs. even harmonics: Kim et al., 2007; 2011). This relates to early interpretations of the 1st harmonic reflecting asymmetries in responses following on and off stimulation cycles (e.g., Clynes et al., 1964), and the 2nd harmonic being typically dominant with pattern reversal stimulation (see the following section). However, the presence of 3rd, 4th, and further higher harmonics, and their inter-dependence, is indicative of the limits of such an oversimplification in most cases.

Paradigm	Frequency 1	Frequency 2	Overlap	Analysis	References
Single frequency	F	-	-	F and its	Adrian &
A-A-A-A-A-A				harmonics	Matthews
					(1934);
					Regan,
					1989
Multiple frequencies	F ₁ (e.g., 8 Hz)	F ₂ (e.g., 6 Hz)	Any	Exclude	Regan &
$(F_1: A-A-A-A-A)$			coinciding	overlapping	Heron,
$(F_2: B-B-B-B-B)$			harmonics of	harmonics	1969;
			F ₁ and F ₂	from analysis	Regan,
			(e.g., 24 Hz)	of both F ₁ and	1989
				F_2	
Symmetry/asymmetry	2F = stimulus	F = stimulus	F harmonics	Exclude 2F	Tyler &
(A-B-A-B-A-B)	presentation	alternation	coinciding	(even)	Kaitz,
	(symmetry	(asymmetry	with 2F and	harmonics	1977;
	response)	response)	its harmonics	from the	Victor &
				analysis of the	Zemon,
				F (odd)	1985
				harmonics	
Oddball	F = stimulus	F/n = oddball B	F/n harmonics	Exclude F and	Heinrich,
(A-A-A-B-A-A-B)	presentation	presentation,	coinciding	its harmonics	Mell &
		with oddballs	with F and its	from the	Bach
		occurring as	harmonics	analysis of F/n	(2009);
		every n th			Liu-
		stimulus			Shuang,
					Norcia &
					Rossion
					(2014)

Table 1. Identifying specific harmonics for consideration in response analysis, according to different frequency-tagging stimulation paradigms. In the paradigm example sequence illustrations: A = one stimulus or stimulus type; B = another stimulus or stimulus type. *Special

cases: In the case that A and B stimuli in a symmetry/asymmetry paradigm lead to symmetrical brain responses, e.g., if representing pattern-reversals, only even harmonics are observed (Cobb, Morton & Ettlinger, 1967; Hou et al., 2003; Norcia et al., 2015); in a combined symmetry/asymmetry and oddball design (Braddick et al., 2005), the odd harmonic analysis is unaffected. In the case that multiple frequencies lead to intermodulation, i.e., additive and subtractive interaction frequencies and their harmonics, the analysis of the intermodulation harmonics should exclude the overlapping harmonics of F1 and F2 (e.g., Zemon & Ratliff, 1984; Burns, Elsner & Kreitz, 1992; Hou et al., 2003; Applebaum et al., 2009; Boremanse, Norcia & Rossion, 2013; Gordon et al., 2019). In the case that a stepwise sweep design is applied to a symmetry/asymmetry paradigm, this does not affect the harmonic analysis (see Norcia et al., 2015).

Interpreting harmonics

Why are there higher harmonics?

Non-sinusoidal brain responses

Higher harmonic responses represent complex neural responses in the time domain. At a fundamental level, these harmonic responses are like any other frequency-domain representations: they are sine waves described by frequency, amplitude, and phase (**Fig. 2**). While only one sine wave is required to describe a sinusoidal signal in the time domain, a combination of (a lot of) sine waves is required to describe complex signals in the time domain (**Fig. 3**). Frequency-tagged brain responses are periodic in the time domain, and thus only sine waves periodic to their fundamental frequency, i.e., the harmonics, are mathematically available to describe them. Simple brain responses require few harmonics, while complex responses require more harmonics (**Fig. 4**). For example, lower stimulation frequency responses often have more harmonics, since there are relatively more harmonic frequencies available within a relevant frequency range ceiling (**Fig. 5**).

Limitations of a non-linearity account

Higher harmonic responses have often been interpreted as being caused by non-linearities in the stimulus presentation and/or brain responses (e.g., Van der Tweel & Verduyn Lunel, 1964; 1965; Spekreijse, 1969; Regan, 1966; 1989; Troelstra, 1971; Burns, Elsner & Kreitz, 1992; Norcia et al., 2015; Gordon et al., 2019; see also Shapley, 2009). This relates to early attempts to present stimuli perfectly sinusoidally (e.g., a uniform field being modulated sinusoidally in

luminance; since van der Tweel, 1958). The rationale was that if the brain's response to a sinusoidal stimulus was linear at the level of recording, it too would be perfectly sinusoidal in following this stimulus, and would be represented in the frequency domain by a response only at the fundamental frequency, i.e., without higher harmonics (*Frequency-domain representations*). Contrarily, higher harmonic brain responses were produced in most cases, and were attributed to non-linearities in the brain's responses themselves (e.g., non-linear action potential firing, neural population response dynamics, etc.; e.g., Movshon, Thompson & Tolhurst, 1978; Skottun et al., 1991; Shapley, 2009)¹⁰.

However, more recent studies suggest that the amount of non-linearity, or complex temporal frequency content, in stimulus presentation may *not* correspond with the amount of non-linearity in the brain's response at the population level: there was little to no difference in the higher harmonic amplitude distributions in response to (imperfect) sinusoidal *vs.* squarewave (i.e., abrupt on/off) complex stimulus presentation (Burns, Elsner & Kreitz, 1992; Fawcett et al., 2004; Retter & Rossion, 2016a: Dzhelyova, Jacques & Rossion, 2017). Moreover, while the inherent non-linearity of the brain's responses *could* account for higher harmonics, in practice the amplitude of the higher harmonics is not always above noise level (as addressed in the Introduction), or is very low, suggesting only a modest contribution of this factor (*Frequency-tagged responses in the frequency domain*). That being said, one source of complexity in the brain's responses (even those underlying the first harmonic) may be these non-linearities.

What do higher harmonic responses represent?

Higher harmonic responses represent the relevant frequency characteristics of the response in the time domain (e.g., Galambos, Makeig & Talmachoff, 1981; Baker & Hess, 1984; Norcia et al., 1986; Gaume, Vialatte & Dreyfus, 2014; Heinrich, 2010; Retter & Rossion, 2016; Zhou et al., 2016; Zemon & Gordon, 2018; Rossion, Retter & Liu-Shuang, 2020). That is, dynamics of the time domain response best represented at different frequency ranges will produce more amplitude in those frequency ranges in the frequency domain (**Fig. 7**; compare with the frequency-domain representation in **Fig. 3C**; for another example of frequency representations over time, see Makeig

¹⁰ Higher (intermodulation) harmonic responses have then been used to characterize the non-linearities of brain responses, leading to the exclusion of some potential non-linear models in specific cases (e.g., Regan & Regan, 1988b; Victor & Conte, 2000; Hou et al., 2003; Baker & Wade, 2017).

et al., 2002). To visualize the impact of (a range of) individual harmonics, partial-harmonic time-domain reconstructions have been plotted (Baker & Hess, 1984; Sieving et al., 1998). Note that the amplitude distribution of harmonics across frequencies is, however, affected by the fundamental stimulation frequency and the overall amplitude of the signal. Moreover, individual harmonics do not represent independent or temporally separated aspects of a time-domain response (e.g., Retter & Rossion, 2016; Zhou et al., 2016).

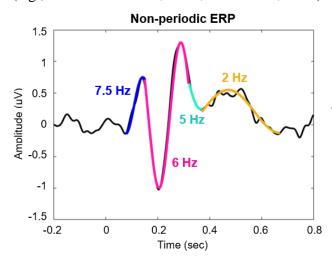


Figure 7. A time-domain signal can be fit with segments of sine waves of different frequencies. While this is not analogous to a frequency transformation, it hints at the range of frequencies that may be optimal for representing this signal (over time).

In line with the above interpretation, harmonic responses may be (gradually) influenced, quantitatively and/or qualitatively, by the frequency at which they fall. For example, Retter & Rossion (2016, Fig. 2C) described harmonic EEG responses that were gradually characterized by frequency, in terms of amplitude and scalp lateralization, commonly across conditions with different, low stimulation frequencies. Harmonic responses may also appear to group into somewhat distinct frequency ranges, e.g., visually-evoked EEG responses above about 10 Hz having a more medial-occipital ("low-level") scalp topography (Rossion, 2014; Jacques, Retter & Rossion, 2016; see also Zemon & Gordon, 2018). In general, higher harmonics may be more associated with earlier response dynamics, as the onset slopes of (ERP) responses are typically steeper than the offsets (Norcia et al., 1986; as in Fig. 7). In some cases, different experimental effects may be pronounced at some harmonic frequencies and not others (e.g., an increased response due to attention: Pei, Pettet & Norcia, 2002; Saupe et al., 2009; opposing effects following current stimulation: Ruhnau et al., 2016). Indeed, limited frequency ranges may be appropriate for measuring certain properties (e.g., a lower frequency range for chromatic than luminance signals; see Burns, Elsner & Kreitz, 1992; Parry et al., 2012). Thus, in addition to

combining harmonics, investigating individual (ranges of) harmonics may provide insight into the functional dynamics of the neural processes that occur at their respective frequencies.

Differing harmonic response distributions may stem from the same fundamental stimulation frequency, such as are observed across conditions (along with time-domain response dynamic differences: e.g., Jacques, Retter & Rossion, 2016; Dzhelyova, Jacques & Rossion, 2017), populations (e.g., clinical: Falsini et al., 1999; Van der Donck et al., 2019; age/grade levels: Hou et al., 2003; van de Walle de Ghelcke et al., 2020) and individuals (as observed in Heinrich & Bach, 2001; Tlumak et al., 2011; Heinrich, Groten & Bach, 2015; used in classifying individuals across testing sessions: Dzhelyova et al., 2019). In past studies, individual harmonic amplitudes have been displayed with frequency-domain spectra or tables, sometimes with additional descriptors, such as functional images or topographies (e.g., Bandettini et al., 1993; Liu-Shuang, Norcia & Rossion, 2014; Jacques, Retter & Rossion, 2016). In more global visualizations, colored/shaded matrices of harmonic responses by regions-of-interest or participant have been plotted (Liu-Shuang, Norcia & Rossion, 2014, Fig. 3; Rossion et al., 2015, Fig. 3), as well as close-shaped "fingerprint" plots, using connected vectors of which the angle is determined by harmonic frequency and length by amplitude (van de Walle de Ghelcke et al., 2020, Fig. 6).

It is not recommended to display harmonics independently by their sequential number (e.g., across different fundamental stimulation frequencies: Troelstra, 1971; Ross et al., 2000; Herrmann, 2001). Indeed, since harmonic responses are characterized by their frequency, they are generally not well characterized by sequential number, irrespective of frequency, unless differentially tagged in the stimulation paradigm (earlier subsection: *Which harmonics to consider?*). However, one case in which harmonic frequency does *not* characterize responses well is at high stimulus presentation frequencies, for which the first harmonic is dominant. At high frequencies, overlapping responses interfere with one another, decreasing the measured response's complexity and amplitude, and therefore harmonic contents (*Frequency-tagged responses in the frequency domain*). Thus, a dominant exponential decrease of harmonic amplitude may be observed across sequential harmonics (compare Fig. 4B&C; Retter et al., 2020, Fig. S2). However, this must not be taken as evidence of distinct brain responses being evidenced at the 1st vs. 2nd (vs. 3rd, etc.) harmonic (e.g., see the discussion of Saupe et al., 2009).

Finally, it may be noted that consecutive response interference is not only dependent upon the duration of the brain response being measured, but is also influenced by the spatio-temporal dynamics of the interfering response components. In models of consecutive responses, destructive superpositioning of overlapping (ERP) response components may reduce or even eliminate (selective harmonic) responses (constructive superpositioning is also possible; see Heinrich, 2010, Figs. 1&2; also Footnote 4). In practice, overlapping brain responses do not occur independently of one another (see Keysers & Perrett, 2002; Retter et al., 2020). However, particularly when distinct response sources are implicated (e.g., light- and dark-preferring neural populations; or across sensory modalities), differential interactions of stimulation frequency and selective harmonic amplitudes could also provide insights into the underlying dynamics of the brain responses.

Should higher harmonic responses be combined, and if so, how? (Reprise)

Limiting the analysis of frequency-tagged responses to a (non-predominant) fundamental harmonic is not recommended: taking harmonic responses into account leads to substantially improved response quantification and classification (**Fig. 8**; Davilda, Srebo & Ghaleb, 1998; Muller-Putz et al., 2005; Cebulla, Stürzebecher & Elberling, 2006; Tlumak et al., 2011; Chen et al., 2015; Retter & Rossion, 2016; Zemon & Gordon, 2018; Cetin, Ozekes & Varol, 2020). The combination of harmonic amplitudes through summation is justified through the principles of frequency-based analyses, and it leads to a combined response measurement that relates to typical time-domain amplitude measurements. It is useful for comparing brain response amplitudes overall, especially those with different temporal dynamics or following different stimulus presentation rates. Note that it is does not preclude, but rather is complementary, to the description of harmonic responses individually.

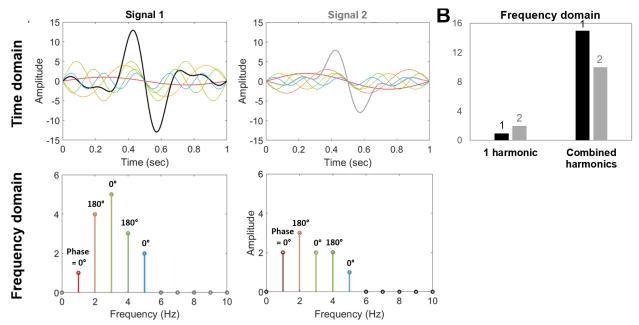


Figure 8. Combining higher harmonics in frequency-domain analyses, expanded from **Fig. 1**. **A) Row 1**: Two periodic signals (thick lines), with their five constituent harmonic frequencies (in thin lines, with colors corresponding to the frequencies below). **Row 2**: Frequency-domain representations of these signals. **B)** In the frequency domain, a consideration of only the fundamental harmonic describes signal 2 as (two times) larger than signal 1. A summation of the five harmonic amplitudes more appropriately describes signal 1 as (50%) larger than signal 2.

Conclusion

Stimuli that are presented periodically generate periodic responses of the brain that are often complex, i.e., non-sinusoidal. To capture and describe these complex brain responses overall, (baseline-corrected) frequency-tagged harmonic response amplitude can be combined through simple summation.

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Competing interests

None.

References

- Adrian, E. D. & Matthews, B. H. C. (1934). The Berger rhythm: Potential changes from the occipital lobes in man. *Brain*, *4*(57), 355–385.
- Adrian, E.D. (1944). Brain Rhythms. *Nature*, 153, 360-362. https://doi.org/10.1038/153360a0
- Ales, J., Farzin, F., Rossion, B., Norcia, A.M. (2012). An objective method for measuring face detection thresholds using the sweep steady-state evoked response. Journal of Vision, 12(10):18, 1–18. https://doi.org/10.1167/12.10.18
- Alonso-Prieto, E. A., Van Belle, G., Liu-Shuang, J., Norcia, A. M. & Rossion, B. (2013). The 6Hz fundamental frequency rate for individual face discrimination in the right occipitotemporal cortex. *Neuropsychologia*, 51, 2863-2975. http://dx.doi.org/10.1016/j.neuropsychologia.2013.08.018
- Anderson, S. K. & Müller, M. M. (2010). Behavioral performance follows the time course of neural facilitation and suppression during cued shifts of feature-selective attention. *PNAS*, 107(31), 13878-13882. https://doi.org/10.1073/pnas.1002436107
- Appelbaum, L. G., Wade, A. R., Vildavski, V. Y., Pettet, M. W., & Norcia, A. M. (2006). Cue-invariant networks for figure and background processing in human visual cortex. *Journal of Neuroscience*, 26(45), 11695–11708. https://doi.org/10.1523/JNEUROSCI.2741-06.2006
- Appelbaum, L. G., Ales, J. M., Cottereau, B. & Norcia, A. M. (2010). Configural specificity of the lateral occipital cortex. *Neuropsychologia*, *48*(11), 3323-3328. https://doi.org/10.1016/j.neuropsychologia.2010.07.016
- Bach, M. & Meigen, T. (1999). Do's and don'ts in Fourier analysis of steady-state potentials. *Documenta Ophthalmologica*, 99(1), 69–82. https://doi.org/10.1023/A:1002648202420
- Baker Jr., C. L. & Hess, R. F. (1984). Linear and nonlinear components of human electroretinogram. *Journal of Neurophysiology*, 51(5), 952-967. https://doi.org/10.1152/jn.1984.51.5.952

- Baker, D. H. & Wade, A. R. (2017). Evidence for an optimal algorithm underlying signal combination in human visual cortex. *Cerebral Cortex*, 27(1), 254-264. https://doi.org/10.1093/cercor/bhw395
- Bandettini, P. A., Jesmanowicz, A., Wong, E. C. & Hyde, J. S. (1993). Processing strategies for time-course data set in functional MRI of the human brain. *Magnetic Resonance in Medicine*, 30(2), 161-173. https://doi.org/10.1002/mrm.1910300204
- Bandetinni, P. A., Jesmanowicz, A., Wong, E. C. & Hyde, J. S. (1993). Processing strategies for time-course data sets in functional MRI of the human brain. *Magnetic Resonance in Medicine*, 30(2), 161–173. https://doi.org/10.1002/mrm.1910300204
- Başar, E. & Schürmann, M. (1994). Functional aspects of evoked alpha and theta responses in humans and cats. *Biological Cybernetics*, 72, 175–183. https://doi.org/10.1007/BF00205981
- Beck, A. A., Rossion, B., & Samson, D. (2018). An objective neural signature of rapid perspective taking. *Social cognitive and affective neuroscience*, *13*(1), 72–79. https://doi.org/10.1093/scan/nsx135
- Bekhtereva, V., Pritschmann, R., Keil, A. & Müller, M. M. (2018). The neural signature of extracting emotional content from rapid visual streams at multiple presentation rates: A cross-laboratory study. *Psychophysiology*, *55*(12), e13222. https://doi.org/10.1111/psyp.13222
- Boremanse, A., Norcia, A.M., Rossion, B. (2013). An objective signature for visual binding of face parts in the human brain. *Journal of Vision* (11):6, 1-18. https://doi.org/10.1167/13.11.6
- Braddick, O., Birtles, D., Wattam-Bell, J. & Atkinson, J. (2005). Motion- and orientation-specific cortical responses in infancy. *Vision Research*, 45(25-26), 3169-79. https://doi.org/10.1016/j.visres.2005.07.021
- Brazier, M. A. B. (1964). A study of the variability of response to flicker: the influence of other sensory stimuli. *Documenta Ophthalmologica*, *18*, 221–237. https://doi.org/10.1007/BF00160575
- Burns, S. A., Elsner, A. E. & Kreitz, M. R. (1992). Analysis of nonlinearities in the flicker ERG. *Optometry and Vision Science*, 69(2), 95-105. https://doi.org/10.1097/00006324-199202000-00002

- Capilla, A., Pazo-Alvarez, P., Darriba, A., Campo, P., & Gross, J. (2011). Steady-state visual evoked potentials can be explained by temporal superposition of transient event-related responses. *PloS one*, *6*(1), e14543. https://doi.org/10.1371/journal.pone.0014543
- Cebulla, M., Stürzebecher, E. & Elberling, C. (2006). Objective detection of auditory steady-state responses: comparison of one-sample and q-sample tests. Journal of the American Academy of Audiology, 17(2), 93-103. https://doi.org/10.3766/jaaa.17.2.3
- Cetin, V., Ozekes, S. & Varol, H. S. (2020). Harmonic analysis of steady-state visual evoked potentials in brain computer interfaces. *Biomedical Signal Processing and Control*, 60, 101999, 1-6.
- Chadnova, E., Reynaud, A., Clavagnier, S., Baker, D. H., Baillet, S., & Hess, R. F. (2018). Interocular interaction of contrast and luminance signals in human primary visual cortex. *NeuroImage*, 167, 23–30. https://doi.org/10.1016/j.neuroimage.2017.10.035
- Chemin, B., Huang, G., Mulders, D. & Mouraux, A. (2018). EEG time-warping to study non-strictly-periodic EEG signals related to the production of rhythmic movements. *Journal of Neuroscience Methods*, 308, 106-115. https://doi.org/10.1016/j.jneumeth.2018.07.016
- Chen, Y., Seth, A. K., Gally, J. A. & Edelman, G. M. (2003). The power of human brain magnetoencephalographic signals can be modulated up or down by changes in an attentive visual task. *Proceedings of the National Academy of Sciences*, 100(6), 3501-3506. https://doi.org/10.1073/pnas.0337630100
- Chen, X., Wang., J., Nakanishi, M., Gao, X., Jung, T.-P. & Gao, S. (2015). High-speed spelling with a noninvasive brain—computer interface. *PNAS*, 112(44), E6058-E6067. https://doi.org/10.1073/pnas.1508080112
- Cheng, M., Gao, X., Gao, S. & Xu, D. (2002). Design and implementation of a brain-computer interface with high transfer rates. *IEEE Transactions on Biomedical Engineering*, 49(10), 1181-1186. https://doi.org/10.1109/TBME.2002.803536
- Clynes, M., Kohn, M. & Lifshitz, K. (1964). Dynamics and spatial behavior of light evoked potentials, their modification under hypnosis, and on-line correlation in relation to rhythmic components. *Annals of the New York Academy of Sciences*, 112, 468-509. https://doig.org/10.1111/j.1749-6632.1964.tb26764.x

- Cobb, W. A., Morton, H. B. & Ettlinger, G. (1967). Cerebral potentials evoked by pattern reversal and their suppression in visual rivalry. *Nature*, *216*(5120), 1123–1125. https://doi.org/10.1038/2161123b0
- Coia, A. & Jones, C. & Duncan, C. & Crognale, M. (2014). Physiological correlates of watercolor effect. *Journal of the Optical Society of America. A, Optics, Image Science, and Vision. 31.* A15-22. https://doi.org/10.1364/JOSAA.31.000A15
- Cottereau, B., Lorenceau, J., Gramfort, A., Clerc, M., Thirion, B., & Baillet, S. (2011). Phase delays within visual cortex shape the response to steady-state visual stimulation.

 NeuroImage, 54(3), 1919–1929. https://doi.org/10.1016/j.neuroimage.2010.10.004
- Cunningham, D. G. M., Baker, D. H. & Pierce, J. W. (2017). Measuring nonlinear signal combination using EEG. *Journal of Vision*, 17(5): 10. https://doi.org/10.1167/17.5.10
- Damon, F., Leleu, A., Rekow, D., Foncet, F. & Baudouin, J-Y. (2020). Expertise for conspecific face individuation in the human brain. *NeuroImage*, 204, 116218. https://doi.org/10.1016/j.neuroimage.2019.116218
- Danielson, G. C., and Lanczos, C. (1942). Some improvements in practical Fourier analysis and their application to X-ray scattering from liquids. *J. Franklin Inst.*, 233(4), 365–380. https://doi.org/10.1016/S0016-0032(42)90767-1
- Davidson, M. J., Mithen, W., Hogendoorn, H., van Boxtel, J. J.-A., Tsuchiya, N. (2020). The SSVEP tracks attention, not consciousness, during perceptual filling-in. *eLife*, e60031, 1-26. https://doi.org/10.7554/eLife.60031
- Davila, C. E., Srebro, R. & Ghaleb, I. A. (1998). Optimal detection of visual evoked potentials. *IEEE Transactions on Bio-Medical Engineering*, 45(6), 800–803. https://doi.org/10.1109/10.678615
- De Keyser, R., Mouraux, A., Quek, G.L. *et al.* Fast periodic visual stimulation to study tool-selective processing in the human brain. *Experimental Brain Research*, *236*, 2751–2763 (2018). https://doi.org/10.1007/s00221-018-5331-2
- Delorme, A. & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9-21. https://doi.org/10.1016/j.jneumeth.2003.10.009

- Di Russo, F., Teder-Salajarvi, W. A. & Hillyard, S. A. (2002). Steady-State VEP and Attentional Visual Processing. In A. Zani & A. Proberbio (Eds.), *The Cognitive Electrophysiology of Mind and Brain*, pp. 257-272. Academic Press.
- Di Russo, F., Pitzalis, S., Aprile, T., Spitoni, G., Patria, F., Stella, A., Spinelli, D., & Hillyard, S. A. (2007). Spatiotemporal analysis of the cortical sources of the steady-state visual evoked potential. *Human Brain Mapping*, 28(4), 323–334. https://doi.org/10.1002/hbm.20276
- Ding, J., Sperling, G. & Srinivasan, R. (2006). Attentional modulation of SSVEP power depends on the network tagged by the flicker frequency. *Cerebral Cortex*, 16(7), 1016–1029. https://doi.org/10.1093/cercor/bhj044
- Donker, D. N. J. (1975). Harmonic composition and topographic distribution of responses to sine wave modulated light (SML), their reproducibility and their interhemispheric relationship. *Electroencephalography and Clinical Neurophysiology*, *39*, 561-574.
- Dwyer, P., Xu, B. & Tanaka, J. W. (2019). Investigating the perception of face identity in adults on the autism spectrum using behavioural and electrophysiological measures. *Vision Research*, 157, 132-141. https://doi.org/10.1016/j.visres.2018.02.013
- Dzhelyova, M. & Rossion, B. (2014). Supra-additive contribution of shape and surface information to individual face discrimination as revealed by fast periodic visual stimulation. *Journal of Vision*, 14(14):15, 1–14. https://doi.org/10.1167/14.14.15
- Dzhelyova, M. & Rossion, B. (2014b). The effect of parametric stimulus size variation on individual face discrimination indexed by fast periodic visual stimuliation. BMC *Neuroscience*, 15:87, 1-12. https://doi.org/10.1186/1471-2202-15-87
- Dzhelyova, M., Jacques, C. & Rossion, B. (2017). At a single glance: fast periodic visual stimulation uncovers the spatio-temporal dynamics of brief facial expression changes in the human brain. *Cerebral Cortex.* 27(8), 4106-4123. https://doi.org/10.1093/cercor/bhw223
- Dzhelyova, M., Jacques, C., Dormal, G., Michel, C., Schiltz, C. & Rossion, B. (2019). High test-retest reliability of a neural index of rapid automatic discrimination of unfamiliar individual faces. *Visual Cognition*, 27:2, 127-141. https://doi.org/10.1080/13506285.2019.1616639
- Eidelman-Rothman, M., Ben-Simon, E., Freche, D., Keil, A., Hendler, T. & Levit-Binnun, N. (2019). Sleepless and desynchronized: Impaired inter trial phase coherence of steady-state

- potentials following sleep deprivation. *NeuroImage*, 202:116055, 1-9. https://doi.org/10.1016/j.neuroimage.2019.116055
- Engel, S. A., Glover, G. H. & Wandell, B. A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cerebral Cortex*, 7(2), 181-192. https://doi.org/10.1093/cercor/7.2.181
- Falsini, B., Iarossi, G., Fadda, A., Porrello, G., Valentini, P., Piccardi, M. & Scullica, L. (1999). The fundamental and second harmonic of the photopic flicker electroretinogram: temporal frequency-dependent abnormalities in retinitis pigmentosa. *Clinical Neurophysiology*, 110(9), 1554-1562. https://doi.org/10.1016/S1388-2457(99)00106-6
- Fawcett, I. P., Barnes, G. R., Hillebrand, A. & Singh, K. D. (2004). The temporal frequency tuning of human visual cortex investigated using synthetic aperture magnetometry. *NeuroImage*, 21(4), 1542-1553. https://doi.org/10.1016/j.neuroimage.2003.10.045
- Fisher, K., Towler, J., Rossion, B. & Eimer, M. (2020). Neural responses in a fast periodic visual stimulation paradigm reveal domain-general visual discrimination deficits in developmental prosopagnosia. *Cortex*, 133, 76-102. https://doi.org/10.1016/j.cortex.2020.09.008
- Forinash, K., & Christian, W. (2016). *Sound: An Interactive EBook*. Retrieved June 4, 2020, from https://www.compadre.org/books/SoundBook
- Fourier, J. (1822). Théorie analytique de la chaleur. F. Didot père et fils.
- Galambos, R., Makeig, S., & Talmachoff, P. J. (1981). A 40-Hz auditory potential recorded from the human scalp. *Proc Natl Acad Sci U S A.*, 78(4), 2643-2647. https://doi.org/10.1073/pnas.78.4.2643
- Gao, X., Gentile, F. & Rossion, B. (2018). Fast periodic stimulation: a highly effective approach in fMRI brain mapping. *Brain Structure and Function*, 223, 2433-2454 https://doi.org/10.1007/s00429-018-1630-4
- Gaume, A., Vialatte, F. & Dreyfus, G. (2014). Transient brain activity explains the spectral content of steady-state visual evoked potentials. *Conf Proc IEEE Eng Med Biol Soc*, 688-692. https://doi:10.1109/EMBC.2014.6943684
- Geisler, C. D. (1960). Average responses to clicks in man recorded by scalp electrodes. *MIT Research Laboratory of Electronics, Cambridge (Technical Report 380)*.
- Gonzalez, R. & Woods, R. (2018). Digital Image Processing (4th ed.). Pearson.

- Gordon, N., Hohwy, J., Davidson, M. J., van Boxtel, J., & Tsuchiya, N. (2019). From intermodulation components to visual perception and cognition A review. *NeuroImage*, 199, 480–494. https://doi.org/10.1016/j.neuroimage.2019.06.008
- Gruss, L. F., Wieser, M. J., Schweinberger, S. R., & Keil, A. (2012). Face-evoked steady-state visual potentials: Effects of presentation rate and face inversion. *Frontiers of Human Neuroscience*, 6:316. https://doi.org/10.3389/fnhum.2012.00316
- Guillame, M., Mejias, S., Rossion, B., Dzhelyova, M. & Schiltz, C. (2018). A rapid, objective and implicit measure of visual quantity discrimination. *Neuropsychologia*, 111, 180-189. https://doi.org/10.1016/j.neuropsychologia.2018.01.044
- Gwinn, O. S., Matera, C. N., O'Neil, S. F., & Webster, M. A. (2018). Asymmetric neural responses for facial expressions and anti-expressions. *Neuropsychologia*, *119*, 405–416. https://doi.org/10.1016/j.neuropsychologia.2018.09.001
- Gwinn, O.S & Jiang, F. (2019). Hemispheric asymmetries in deaf and hearing during sustained peripheral selective attention. *Journal of Deaf Studies and Deaf Education*, 25(1), 1-9. https://doi.org/10.1093/deafed/enz030
- Heinrich, S. P. & Bach, M. (2001) Adaptation dynamics in pattern-reversal visual evoked potentials. *Documenta Ophthalmologica*, 102, 141–156. https://doi.org/10.1023/A:1017509717071
- Heinrich, S.P. (2009). Permutation-Based Significance Tests for Multiharmonic Steady-State Evoked Potentials. *IEEE Transactions on Biomedical Engineering*, 56, 534-537. https://doi.org/10.1109/TBME.2008.2006021
- Heinrich, S. P., Mell, D. & Bach, M. (2009). Frequency-domain analysis of fast oddball responses to visual stimuli: a feasibility study. *International Journal of Psychophysiology:* Official journal of the International Organization of Psychophysiology, 73(3), 287–293. https://doi.org/10.1016/j.ijpsycho.2009.04.011
- Heinrich, S. P. (2010). Some thoughts on the interpretation of steady-state evoked potentials. *Documenta Ophthalmologica*, 120, 205-214. http://dx.doi.org/10.1007/s10633
- Heinrich, S. P., Groten, M. & Bach, M. (2015). Relating the steady-state visual evoked potential to single-stimulus responses derived from m-sequence stimulation. *Documenta Opthalmologica*, 131(1), 13-24. https://doi.org/10.1007/s10633-015-9492-z

- Herrmann, C. (2001). Human EEG responses to 1–100 Hz flicker: resonance phenomena in visual cortex and their potential correlation to cognitive phenomena. *Experimental Brain Research*, *137*, 346–353. https://doi.org/10.1007/s002210100682
- Herrmann, C. S., Rach, S., Vosskuhl, J. & Strüber, D. (2014). Time-frequency analysis of event-related potentials: a brief tutorial. *Brain Topography*, 27(4), 438-450. https://doi.org/10.1007/s10548-013-0327-5
- Hönegger, C., Atteneder, C., Griesmayr, B., Holz, E., Weber, E. & Sauseng, P. (2011). Neural correlates of visuo-spatial working memory encoding an EEG study. *Neuroscience Letters*, 500(2), 118-122. https://doi.org/10.1016/j.neulet.2011.06.017
- Hou, C., Pettet, M. W., Sampath, V., Candy, T. R. & Norcia, A. M. (2003). Development of the spatial organization and dynamics of lateral interactions in the human visual system. *The Journal of Neuroscience*, 23(25), 8630–8640. https://doi.org/10.1523/JNEUROSCI.23-25-08630.2003
- Hou, C., Pettet, M. W. & Norcia, A. M. (2008). Abnormalities of coherent motion processing in strabismic amblyopia: Visual-evoked potential measurements. *Journal of Vision*, 8(4):2, 1-12. https://doi.org/10.1167/8.4.2
- Jacques, C., Retter, T. L. & Rossion, B. A single glance at a face generates larger and qualitatively different category-selective spatio-temporal signatures than other ecologically-relevant categories in the human brain. *NeuroImage*, 137, 21-33. https://doi.org/10.1016/j.neuroimage.2016.04.045
- Jervis, B. W., Nichols, M. J. Johnson, T. E., Allen, E. and Hudson, N. R. (1983). A Fundamental Investigation of the Composition of Auditory Evoked Potentials. *IEEE Transactions on Biomedical Engineering*, 30(1), 43-50. https://doi.org/10.1109/TBME.1983.325165
- Jonas, J.*, Jacques, C.*, Liu-Shuang, J., Brissart, H., Colnat-Coulbois, S., Maillard, L., Rossion, B. (2016). A face-selective ventral occipito-temporal map of the human brain with intracerebral potentials. *Proc. Natl. Acad. Sci. USA*, 113, E4088-E4097. https://doi.org/10.1073/pnas.1522033113
- Kaspar, K., Hassler, U., Martens, U., Trujillo-Barreto, N. & Gruber, T. (2001). Steady-state visually evoked potential correlates of object recognition. *Brain Research*, 1343, 112-121. https://doi.org/10.1016/j.brainres.2010.04.072

- Katzner, S., Nauhaus, I., Benucci, A., Bonin, V., Ringach, D. L., & Carandini, M. (2009). Local origin of field potentials in visual cortex. *Neuron*, 61(1), 35–41. https://doi.org/10.1016/j.neuron.2008.11.016
- Keitel, C., Quigley, C. & Ruhnau, P. (2014). Stimulus-driven brain oscillations in the alpha range: entrainment of intrinsic rhythms or frequency-following response?. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *34*(31), 10137–10140. https://doi.org/10.1523/JNEUROSCI.1904-14.2014
- Keysers, C. & Perrett, D. I. (2002). Visual masking and RSVP reveal neural competition. *Trends in Cognitive Sciences*, 6(3), 120-125. https://doi.org/10.1016/S1364-6613(00)01852-0
- Kim, Y.-J., Grabowecky, M., Paller, K. et al. (2007). Attention induces synchronization-based response gain in steady-state visual evoked potentials. *Nature Neuroscience*, 10, 117–125. https://doi.org/10.1038/nn1821
- Kim, Y.-J., Grabowecky, M., Paller, K. A. & Suzuki, S. (2011). Differential roles of frequency-following and frequency-doubling visual responses revealed by evoked neural harmonics. *Journal of Cognitive Neuroscience*, 23(8), 1875–1886. https://doi.org/10.1162/jocn.2010.21536
- Kosem, A., Gramfort, A. & Van Wassenhove, V. (2014). Encoding of event timing in the phase of neural oscillations. NeuroImage, 92(15), 274-284. https://doi.org/10.1016/j.neuroimage.2014.02.010
- Kremers, J., & Scholl, H. (2001). Rod-/L-cone and rod-/M-cone interactions in electroretinograms at different temporal frequencies. *Visual Neuroscience*, *18*(3), 339-351. https://doi.org/10.1017/S095252380118301X
- Kremers, J., Rodrigues, A. R., Silveira, L. C., da Silva Filho, M. (2010). Flicker ERGs Representing Chromaticity and Luminance Signals. *Investigative Ophthalmology & Visual Science*, 51(1), 577-587. https://doi.org/10.1167/iovs.09-3899.
- Kuś, R., Duszyk, A., Milanowski, P., Łabęcki, M., Bierzyńska, M., Radzikowska, Z., Michalska, M., Zygierewicz, J., Suffczyński, P. & Durka, P. J. (2013). On the quantification of SSVEP frequency responses in human EEG in realistic BCI conditions. *PloS one*, 8(10), e77536. https://doi.org/10.1371/journal.pone.0077536
- Leleu, A., Dzhelyova, D., Rossion, B., Brochrd, R., Durand, K., Schaal, B. & Baudouin, J.-Y. (2018). Tuning functions for automatic detection of brief changes of facial expression in

- the human brain. *NeuroImage*, 179, 245-251. https://doi.org/10.1016/j.neuroimage.2018.06.048
- Leleu, A., Rekow, D., Poncet, F., Schaal, B., Durand, K., Rossion, B., Baudouin, J.-Y. (2020).

 Maternal odor shapes rapid face categorization in the infant brain. *Developmental Science*.

 23:e12877. https://doi.org/10.1111/desc.12877
- Liu-Shuang, J., Norcia, A.M., Rossion, B. (2014). An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic visual stimulation. *Neuropsychologia*, 52, 57-72. http://dx.doi.org/10.1016/j.neuropsychologia.2013.10.022
- Liu-Shuang, J., Torfs, K., Rossion, B. (2016). An objective electrophysiological marker of face individualisation impairment in acquired prosopagnosia with fast periodic visual stimulation. *Neuropsychologia*, 83, 100-113. https://doi.org/10.1016/j.neuropsychologia.2015.08.023
- Lochy, A., Van Belle, G. & Rossion, B. (2015). A robust index of lexical representation in the left occipito-temporal cortex as evidenced by EEG responses to fast periodic visual stimulation. *Neuropsychologia*, *66*, 18-31. http://dx.doi.org/10.1016/j.neuropsychologia.2014.11.007
- Lochy, A., Van Reybroeck, M., Rossion, B. (2016). Left cortical specialization for visual letter strings predicts rudimentary knowledge of letter-sound association in preschoolers. *Proc. Natl. Acad. Sci. USA*, 113, 8544-8549. https://doi.org/10.1073/pnas.1520366113
- Lochy, A., Schiltz, C., Rossion, B. (2020). The right hemispheric dominance for face perception in preschool children depends on visual discrimination level. *Developmental Science*, 23(3):e12914. https://doi.org/10.1111/desc.12914
- Luck, S. J. (2005). *An Introduction to the Event-Related Potential Technique*. Cambridge, MA: MIT Press.
- Makeig, , S., Westerfield, M., Jung, T.-P., S. Enghoff, S., Townsend, J., Courchesne, E. & Sejnowski, T. J. (2002). Dynamic brain sources of visual evoked responses. *Science*, 295(5555), 690-694. https://doi.org/10.1126/science.1066168
- McFadden, K. L, Steinmetz, S. E., Carroll, A., M., Simon, S. T., Wallace, A. et al. (2014). Test-retest reliability of the 40 Hz EEG auditory steady-state response. PLOS ONE, 9(1): e85748. https://doi.org/10.1371/journal.pone.0085748

- McKeefry, D. J., Russell, M. H., Murray, I. J. & Kulikowski, J. J. (1996). Amplitude and phase variations of harmonic components in human achromatic and chromatic visual evoked potentials. *Visual Neuroscience*, 13(4), 639-653. https://doi.org/10.1017/s0952523800008543
- Meigen, T. & Bach, M. (2000). On the statistical significance of electrophysiological steady-state responses. *Documenta Ophthalmologica*, *98*, 207–232. https://doi.org/10.1023/A:1002097208337
- Milton, A., Rowland, A., Stothart, G., Clatworthy, P., Pennington, C. M. & Kazanina, N. (2020). Fast Periodic Visual Stimulation indexes preserved semantic memory in healthy ageing. *Scientific Reports*, 10:13159, 1-10 . https://doi.org/10.1038/s41598-020-69929-5
- Min, B. K., Dähne, S., Ahn, M. H., Noh, Y-.K. & Müller, K.-R. (2016). Decoding of top-down cognitive processing for SSVEP-controlled BMI. *Scientific Reports*, 6:36267, 1-11. https://doi.org/10.1038/srep36267
- Miskociv, V. & Keil, A. (2013). Perceiving threat in the face of safety: Excitation and inhibition of conditioned fear in human visual cortex. *Journal of Neuroscience*, 33(1), 72-78. https://doi.org/10.1523/JNEUROSCI.3692-12.2013
- Morgan, S. T., Hansen, J. C. & Hillyard, S. A. (1996). Selective attention to stimulus location modulates the steady-state visual evoked potential. *PNAS USA*, 93, 4770-4774. https://doi.org/10.1073%2Fpnas.93.10.4770
- Moungou, A., Thonnard, J.-L. & Mouraux, A. (2016). EEG frequency tagging to explore the cortical activity related to the tactile exploration of natural textures. *Scientific Reports*, 6:20738. https://doi.org/10.1038/srep20738
- Mouraux, A., Iannetti, G. D., Colon, E., Nozaradan, S., Legrain, V. & Plaghki, L. (2011).

 Nociceptive steady-state evoked potentials elicited by rapid periodic thermal stimulation of cutaneous nociceptors. *The Journal of Neuroscience*, *31*(16), 6079–6087.

 https://doi.org/10.1523/JNEUROSCI.3977-10.2011
- Movshon, J. A., Thompson, I. D. & Tolhurst, D. J. (1978), Receptive field organization of complex cells in the cat's striate cortex.. *The Journal of Physiology*, 283(1), 79-99. https://doig.org/10.1113/jphysiol.1978.sp012489

- Müller, M. M., Teder, W. & Hillyard, S. A. (1997). Magnetoencephalographic recording of steadystate visual evoked cortical activity. Brain Topography, 9(3), 163–168. https://doi.org/10.1007/BF01190385
- Müller, M. M., Picton, T. W., Valdes-Sosa, P., Riera, J., Teder-Sälejärvi, W. A. & Hillyard, S. A. (1998). Effects of spatial selective attention on the steady-state visual evoked potential in the 20–28 Hz range. *Cognitive Brain Research*, 6(4), 249-261. https://doi.org/10.1016/S0926-6410(97)00036-0
- Müller, M. M., Andersen, S., Trujillo, N. J., ValdesSosa, P., Malinowski, P., & Hillyard, S. A. (2006). Feature-selective attention enhances color signals in early visual areas of the human brain. *Proceedings of the National Academy of Sciences, USA, 103(38)*, 14250–14254. https://doi.org/10.1073/pnas.0606668103
- Muller-Putz, G. R., Scherer, R., Brauneis, C. & Pfurtscheller, G. (2005). Steady-state visual evoked potential (SSVEP)-based communication: impact of harmonic frequency components. *Journal of Neural Engineering*, 2(4), 123-130. https://doi.org/10.1088/1741-2560/2/4/008
- Norcia, A. M., Sato, T., Shinn, P. & Mertus, J. (1986). Methods for the identification of evoked response components in the frequency and combined time/frequency domains. *Electoencephalography and Clinical Neurophysiology*, 65(3), 212-226. https://doi.org/10.1016/0168-5597(86)90056-0
- Norcia, A. M., Tyler, C. W., Hamer, R. D. & Wesemann, W. (1989). Measurement of spatial contrast sensitivity with the swept contrast VEP. *Vision Research*, 29(5), 627-637. https://doi.org/10.1016/0042-6989(89)90048-5
- Norcia, A.M., Appelbaum, L.G., Ales, J.M., Cottereau, B., Rossion, B. (2015). The steady-state visual evoked potential in vision research: a review. *Journal of Vision*, 15(6):4, 1-46. https://doi.org/10.1167/15.6.4
- Painter, D. R., Dux, P. E., Travis, S. L., & Mattingley, J. B. (2014). Neural responses to target features outside a search array are enhanced during conjunction but not unique-feature search. Journal of Neuroscience, 34(9), 3390–3401. https://doi.org/10.1523/JNEUROSCI.3630-13.2014

- Park, J. (2018). A neural basis for the visual sense of number and its development: A steady-state visual evoked potential study in children and adults. *Developmental Cognitive Neuroscience*, 30, 333-343. https://doi.org/10.1016/j.dcn.2017.02.011
- Parry, N. R., Murray, I. J., Panorgias, A., McKeefry, D. J., Lee, B. B. & Kremers, J. (2012). Simultaneous chromatic and luminance human electroretinogram responses. *Journal of Physiology*, 590(13), 3141-3154. https://doi.org/10.1113/jphysiol.2011.226951
- Parseval des Chênes, M.-A. (1806). Mémoire sur les séries et sur l'intégration complète d'une équation aux différences partielles linéaire du second ordre, à coefficients constants.

 Mémoires présentés à l'Institut des Sciences, Lettres et Arts, par divers savants, et lus dans ses assemblées : Sciences, Mathématiques et Physiques, 1, 638–648.
- Pastor, M. A., Artieda, J., Arbizu, J., Marti-Climent, J. M., Peñuelas, I. & Masdeu, J. C. (2002). Activation of human cerebral and cerebellar cortex by auditory stimulation at 40 Hz. *Journal of Neuroscience*, 22(23), 10501-10506. https://doi.org/10.1523/JNEUROSCI.22-23-10501.2002
- Pastor, M. A., Artieda, J., Arbizu, J., Valencia, M. & Masdeu, J. C. (2003). Human cerebral activation during steady-state visual-evoked responses. *Journal of Neuroscience*, 23(37), 11621-11627. https://doi.org/10.1523/JNEUROSCI.23-37-11621.2003
- Pastor, M. A., Valencia, M., Artieda, J., Alegre, M. & Masdeu, J. C. (2007). Topography of Cortical Activation Differs for Fundamental and Harmonic Frequencies of the Steady-State Visual-Evoked Responses. An EEG and PET H₂¹⁵O Study. *Cerebral Cortex*, 17(8), 1899-1905. https://doi.org/10.1093/cercor/bhl098
- Patel, M. R. (2012). Introduction to Electrical Power and Power Electronics. CRC Press.
- Paulk, A. C., Kirszenblat, L., Zhou, Y. & van Swinderen, B. (2015). Closed-loop behavioral control increases coherence in the fly brain. *Journal of Neuroscience*, *35*(28), 10304-10315. https://doi.org/10.1523/JNEUROSCI.0691-15.2015
- Pei, F., Pettet, M. W. & Norcia, A. M. (2002). Neural correlates of object-based attention. *Journal of Vision*, 2, 588-596. https://doi.org/10.1167/2.9.1
- Peli, E., McCormack, G. & Sokol, S. (1988). Signal to noise ratio considerations in the analysis of sweep visual-evoked potentials. *Applied Optics*, 27(6), 1094-1098. https://doi.org/10.1364/AO.27.001094

- Peterzell, D. H. & Norcia, A. M. (1997). Spatial frequency masking with the sweep-VEP. *Vision Research*, *37*, 2349-2359. https://doi.org/10.1016/s0042-6989(97)00046-1
- Press, W. H., Falnnery, B. P. & Teukolsky, S. A. (1993). *Numerical Recipes in Fortran 77: The Art of Scientific Computing* (2nd ed.). Cambridge University Press.
- Puce, A., Allison, T., Gore, J. C. & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology*, 74(3), 1192-1199. https://doi.org/10.1152/jn.1995.74.3.1192
- Regan, D. (1966). Some characteristics of average steady-state and transient responses evoked by modulated light. *Electroencephalography and Clinical Neurophysiology*, 20(3), 238–248.
- Regan, D. (1975). Colour coding of pattern responses in man investigated by evoked potential feedback and direct plot techniques. *Vision Research*, 15, 175-183. https://doi.org/10.1016/0042-6989(75)90205-9
- Regan, D & Heron, J. R. (1969). Clinical investigation of lesions of the visual pathway: a new objective technique. *Journal of Neurology, Neurosurgery & Psychiatry*, 32, 479-483. https://doi.org/10.1136/jnnp.32.5.479
- Regan, D. & Regan, M. P. (1988). Nonlinearity in human visual responses to two-dimensional patterns, and a limitation of Fourier methods. *Vision Research*, 27(12), 2181-2183. https://doi.org/10.1016/0042-6989(87)90132-5
- Regan, M. P. & Regan, D. (1988b). A frequency domain technique for characterizing nonlinearities in biological systems. *Journal of Theoretical Biology, 133*, 293–317. https://doi.org/10.1016/S0022-5193(88)80323-0
- Regan, D. (1989). Human brain electrophysiology: Evoked potentials and evoked magnetic fields in science and medicine. Elsevier: New York.
- Retter, T. L. & Rossion, B. (2016). Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. *Neuropsychologia*, 91, 9-28. http://dx.doi.org/10.1016/j.neuropsychologia.2016.07.028
- Retter, T. L. & Rossion, B. (2016b). Visual adaptation provides objective electrophysiological evidence of facial identity discrimination. *Cortex*, 80, 35-50. https://doi.org/10.1016/j.cortex.2015.11.025

- Retter, T. L. & Rossion, B. (2017). Visual adaptation reveals an objective electrophysiological measure of high-level individual face discrimination. *Scientific Reports*, 7:3269, 1-10. https://doi.org/10.1038/s41598-017-03348-x
- Retter, T. L., Webster, M. A. & Jiang, F. (2019). Directional visual motion is represented in the auditory and association cortices of early deaf individuals. *Journal of Cognitive Neuroscience*, *31*(8), 1126-1140. https://doi.org/10.1162/jocn_a_01378
- Retter, T., L. Jiang, F., Webster, M.A., Rossion, B. (2020). All-or-none visual categorization in the human brain. *NeuroImage*, 213:116685, 1-16. https://doi.org/10.1016/j.neuroimage.2020.116685
- Ross, B., Borgmann, C., Draganova, R., Roberts, L. E. & Pantev, C. (2000). A high-precision magnetoencephalographic study of human auditory steady-state responses to amplitude-modulated tones. *Journal of the Acoustical Society of America*, 108(2), 679-691. https://doi.org/10.1121/1.429600
- Rossion, B. & Boremanse, A. (2011). Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. Journal of Vision. 11(2):16, 1–21. https://doi.org/10.1167/11.2.16
- Rossion, B., Alonso-Prieto, E., Boremanse, A., Kuefner, D. & Van Belle, G. (2012). A steady-state visual evoked potential approach to individual face perception: effect of inversion, contrast-reversal and temporal dynamics. *NeuroImage*, 63, 1585-1600. https://doi.org/10.1016/j.neuroimage.2012.08.033
- Rossion, B. (2014). Understanding individual face discrimination by means of fast periodic visual stimulation. *Experimental Brain Research*, 232, 1599-1621. https://doi.org/10.1007/s00221-014-3934-9
- Rossion, B., Torfs, K., Jacques, C., Liu-Shuang, J. (2015). Fast periodic presentation of natural face images reveals a robust face-selective electophysiological response in the human brain. *Journal of Vision*, *15*, 1, 18. https://doi.org/10.1167/15.1.18
- Rossion, B., Retter, T. L. & Liu-Shuang, J. (2020). Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. *European Journal of Neuroscience*.
- Ruhnau, P., Keitel, C., Lithari, C., Weisz, N. & Neuling, T. (2016). Flicker-driven responses in visual cortex change during matched-frequency transcranial alternating current stimulation.

- Frontiers in Human Neuroscience, 10:184, 1-13. https://doi.org/10.3389/fnhum.2016.00184
- Saupe, K., Schröger, E., Andersen, S. K. & Müller, M. M. (2009). Neural mechanisms of intermodal sustained selective attention with concurrently presented auditory and visual stimuli. *Frontiers in Human Neuroscience*, 3:58, 1-13. https://doi.org/10.3389/neuro.09.058.2009
- Schettino, A., Porcu, E., Gundlach, C., Keitel, C., & Müller, M. M. (2020). Rapid processing of neutral and angry expressions within ongoing facial stimulus streams: Is it all about isolated facial features?. *PloS one*, 15(4), e0231982. https://doi.org/10.1371/journal.pone.0231982
- Shapley, R. (2009). Linear and nonlinear systems analysis of the visual system: why does it seem so linear? A review dedicated to the memory of Henk Spekreijse. *Vision Research*, 49(9), 907-921. https://doi.org/10.1016/j.visres.2008.09.026
- Sieving, P. A., Arnold, E. B., Jamison, J., Liepa, A. & Coats, C. (1998). Submicrovolt flicker electroretinogram: cycle-by-cycle recording of multiple harmonics with statistical estimation of measurement uncertainty. *Investigative Ophthalmology & Visual Science*, 39(8), 1462-1469.
- Skottun, B. C., De Valois, R. L., Grosof, D. H., Movshon, A., Albrecht, D. G. & Bonds, A. B. (1991). Classifying simple and complex cells on the basis of response modulation. *Vision Research*, 31(7/8), 1079-1086. https://doi.org/10.1016/0042-6989(91)90033-2
- Smith, S. W. (1997). *The Scientist and Engineer's Guide to Digital Signal Processing* (2nd ed.). California Technical Publishing.
- Spekreijse, H. (1969). Rectification in the goldfish retina: Analysis by sinusoidal and auxiliary stimulation. *Vision Research*, 9, 1461–1472.
- Srinivasan, R., Russell, D. P., Edelman, G. M. & Tononi, G. (1999). Increased synchronization of neuromagnetic responses during conscious perception. *Journal of Neuroscience*, *19*(*13*), 5435–5448.
- Strang, G. (2007). Computational Science and Engineering. Wellesley-Cambridge Press.
- Strasburger, H. (1987). The analysis of steady state evoked potentials revisited. *Clinical Vision Science*, *1*(3), 245–256.

- Tang, Y., & Norcia, A. M. (1995). An adaptive filter for steady-state evoked responses. *Electroencephalography and Clinical Neurophysiology*, 96(3), 268–277. https://doi.org/10.1016/0168-5597(94)00309-3
- Tlumak, A. I., Durrant, J. D., Delgado, R. E. & Robert Boston, J. (2011). Steady-state analysis of auditory evoked potentials over a wide range of stimulus repetition rates: Profile in adults. *International Journal of Audiology*, 50(7), 448-458.

 https://doi.org/10.3109/14992027.2011.560903
- Tononi, G., Srinivasan, R., Russell, D. P. & Edelman, G. M. (1998). Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proceedings of the National Academy of Sciences, USA*, 95(6), 3198–3203.
- Troelstra, A. (1971). Harmonic distortion in the frog's ERG and its possible relation to differences in latencies. *Vision Research*, 11, 393-403. https://doi.org/10.1016/0042-6989(71)90082-4
- Tyler, C. W., & Kaitz, M. (1977). Movement adaptation in the visual evoked response. *Experimental Brain Research*, 27(2), 203–209. https://doi.org/10.1007/BF00237698
- Van der Tweel, L. H., Sem-Jacobson, C. W., Kamp, A., Storm van Leeuwen, W., & Veringa, F.
 T. H. (1958). Objective determination of response to modulated light. *Acta physiologica et pharmacologica Neerlandica*, 7, 528-529.
- Van der Tweel, L. H. (1964). Relation between psychophysics and electrophysiology of flicker. *Documenta ophthalmologica*, *18*, 287–304. https://doi.org/10.1007/BF00160581
- Van der Tweel, L. H. & Verduyn Lunel, H. F. E. V. (1965). Human visual responses to sinusoidally modulated light. *Electroencephalography and Clinical Neurophysiology*, 18(6), 587-598. https://doi.org/10.1016/0013-4694(65)90076-3
- van de Walle de Ghelcke, A., Rossion, B., Schiltz, C. & Lochy, A. (2021). Developmental changes in letter-selective neural sensitivity: a one-year follow-up of beginning readers. *Developmental Science*, 00:e12999. https://doi.org/10.1111/desc.12999
- Van der Donck, S., Dzhelyova, M., Vettori, S., Thielen, H., Steyaert, J., Rossion, B. & Boets, B. (2019). Fast periodic visual stiulation EEG reveals reduced neural sensitivity to fearful faces in children with Autism. *Journal of Autism and Developmental Disorders*, 49, 4658-4673. https://doi.org/10.1007/s10803-019-04172-0

- Vialatte, F.-B., Maurice, M., Dauwels, J. & Cichocki, A. (2009). Steady state visual evoked potentials in the delta range (0.5-5 Hz). *ICONIP*, 1:5506, 399-406.
- Vialatte, F. B., Maurice, M., Dauwels, J. & Cichocki, A. (2010). Steady-state visually evoked potentials: Focus on essential paradigms and future perspectives. *Progress in Neurobiology*, 90(4), 418–438. https://doi.org/10.1016/j.pneurobio.2009.11.005
- Victor, J. D. & Conte, M. M. (2000). Two-frequency analysis of interactions elicited by Vernier stimuli. *Visual Neuroscience*, *17*, 959-973. https://doi.org/10.1017/s0952523800176151
- Victor, J. D. & Zemon, V. (1985). The human visual evoked potential: Analysis of components due to elementary and complex aspects of form. *Vision Research*, *25*(*12*), 1829-1842. https://doi.org/10.1016/0042-6989(85)90006-9
- Wang, B. Y., Gao, X., Hong, B., Jia, C. & Gao, S. (2008). Brain-computer interfaces based on visual evoked potentials. *IEEE Engineering in Medicine and Biology Magazine*, 27(5), 64-71. https://doi.org/10.1109/MEMB.2008.923958
- Watkin, P. (2008). *Auditory Steady-State Response: Generation, Recording, and Clinical Applications*. Ed. G Rance. Plural Publishing.
- Wattam-Bell, J., Birtles, D., Nystrom, P., von Hofsten, C., Rosander, K., Anker, S., Atkinson, J & Braddick, O. (2010). Reorganization of global form and motion processing during human visual development. *Current Biology*, 20(5), 411-415. https://doi.org/10.1016/j.cub.2009.12.020
- Winawer, J., Kay, K. N., Foster, B. L., Rauschecker, A. M., Parvizi, J. & Wandell, B. A. (2013). Asynchronous broadband signals are the principal source of the BOLD response in human visual cortex. Current Biology, 23(13), 1145-1153. https://doi.org/10.1016/j.cub.2013.05.001
- Wittevrongel, B., Khachatryan, E., Hnazaee, M. F., Camarrone, F., Carrette, E., De Taeye, L., et al. (2018). Decoding steady-state visual evoked potentials from electrocorticography. *Frontiers in Neuroinformatics*, 12:65, 1-14. https://doi.org/10.3389/fninf.2018.00065
- Xu, B., Liu-Shuang, J., Rossion, B., Tanaka, J.W. (2017). Individual differences in face identity processing with fast periodic visual stimulation. *Journal of Cognittive Neuroscience*, 29, 1368-1377. https://doi.org/doi:10.1162/jocn_a_01126

- Zemon, V. & Ratliff, F. (1984). Intermodulation components of the visual evoked potential: Responses to lateral and superimposed stimuli. *Biological Cybernetics*, 50, 401–408. https://doi.org/10.1007/BF00335197
- Zemon, V. M. & Gordon, J. (2018). Quantification and statistical analysis of the transient visual evoked potential to a contrast-reversing pattern: a frequency-domain approach. *European Journal of Neuroscience*, 48(2), 1765-1788. https://doi.org/10.1111/ejn.14049
- Zhang, P., Jamison, K., Engel, S., He, B. & He, S. (2011). Binocular rivalry requires visual attention. *Neuron*, 71(2), 362-369. https://doi.org/10.1016/j.neuron.2011.05.035
- Zhou, H., Melloni, L., Poeppel, D. & Ding, N. (2016). Interpretations of frequency domain analyses of neural entrainment: periodicity, fundamental frequency, and harmonics. *Frontiers in Human Neuroscience*, 10:274. https://doi.org/10.3389/fnhum.2016.00274
- Zoefel, B., Oever, S.T., & Sack, A.T. (2018). The involvement of endogenous neural oscillations in the processing of rhythmic input: more than a regular repetition of evoked neural responses. *Frontiers in Neuroscience*, 12. https://doi.org/10.3389/fnins.2018.00095