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Steady-state visually evoked potentials: Focus on essential paradigms and future perspectives

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ABSTRACT

After 40 years of investigation, steady-state visually evoked potentials (SSVEPs) have been shown to be useful for many paradigms in cognitive (visual attention, binocular rivalry, working memory, and brain rhythms) and clinical neuroscience (aging, neurodegenerative disorders, schizophrenia, ophthalmic pathologies, migraine, autism, depression, anxiety, stress, and epilepsy). Recently, in engineering, SSVEPs found a novel application for SSVEP-driven brain–computer interface (BCI) systems. Although some SSVEP properties are well documented, many questions are still hotly debated. We provide an overview of recent SSVEP studies in neuroscience (using implanted and scalp EEG, fMRI, or PET), with the perspective of modern theories about the visual pathway. We investigate the steady-state evoked activity, its properties, and the mechanisms behind SSVEP generation. Next, we describe the SSVEP-BCI paradigm and review recently developed SSVEP-based BCI systems. Lastly, we outline future research directions related to basic and applied aspects of SSVEPs.

Contents

Abbreviations: ALE, adaptive line enhancement; ASSR, auditory steady-state response; BCI, brain–computer interface; Chkb, checkerboard; ICA, independent component analysis; ITR, information transfer rate; KC, koniocellular pathway; LCD, liquid crystal display; LED, light-emitting diode; LGN, lateral geniculate nuclei; MC, magnocellular pathway; NIRS, near-infrared spectroscopy; PC, parvocellular pathway; RGCs, retinal ganglion cells; SEPs, sensory evoked potentials; SNR, signal-to-noise ratio; SSEP, steady-state evoked potentials; SSMP, steady-state somatosensory evoked potentials; SSTP, steady-state topographical probe; SSVEPs, steady-state visual evoked potentials; VEPs, visual evoked potentials; WM, working memory.

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1. Fundamentals of steady-state visually evoked potentials (SSVEPs)

1.1. Introduction

Sensory evoked potentials (SEPs) are electrical potentials, recorded from the central nervous system of humans or animals (usually EEG) while *stimulating* sense organs; they are distinct from *spontaneous* potentials (background EEG), which are recorded without stimulation. Contrary to event-related potentials, SEPs are phase-locked to the stimulus. Therefore, they can be enhanced using averaging techniques over many trials (Dawson, 1954). They can be interpreted as the reorganization of spontaneous brain oscillations in response to a stimulus (Başar, 1980; Başar et al., 1999). Visible outcomes of SEPs can be observed even in single trials (Effern et al., 2000; Quiroga et al., 2001). The mechanism underlying the formation of SEPs when EEG signals are averaged is a matter of debate. Three main theories compete for the interpretation of what constitutes an SEP: simple additive effect of changes occurring in all trials, transient phase resetting of ongoing activity (Klimesch et al., 2007; Moratti et al., 2007), or baseline shift of ongoing activity (Nikulin et al., 2007).

The visual system has received much attention in neuroscience during the last century. From retinal photoreceptors, visual percepts propagate first to the visual areas, and next to the rest of the brain (depending on the stimulus type; see Section 1.2 and Fig. 1).

Following the presentation of visual stimuli, SEPs, termed visually evoked potentials (VEPs), can be recorded in the visual areas. Several types of stimuli can elicit VEPs (see Odom et al., 2004 for review); the most common are flash (luminance) and pattern stimulation (see Fig. 1). A flash VEP is obtained when a uniform flash is used as stimulus, while pattern stimulation corresponds to the use of reversal (pattern reversal VEP) or onset/offset (pattern ON–OFF VEP) of a stimulus (generally a checkerboard). These transient VEPs are well known and appear as a succession of waveforms (Odom et al., 2004):

- Flash-VEPs are much more variable across subjects than pattern responses but show little interocular asymmetry. They consist of a series of negative and positive waves; the most robust components are the N2 (90 ms) and P2 (120 ms) peaks;
- Pattern reversal VEPs have the lowest variability in waveform and peak latency both within a subject and over a normal population. This VEP consists of the N75, P100, and N135 components;
- Pattern offset/onset: more variable in appearance than pattern reversals. This VEP presents three main peaks: C1 (positive, 75 ms), C2 (negative, 125 ms), and C3 (positive, 150 ms).

Note that the peaks (N, P, C) may vary with the age of the subject and that VEPs can be elicited in very young subjects (e.g., Chin et al., 1985 reported VEPs in neonates as young as 24 gestational weeks, using light-emitting diodes as visual stimulation).

1.2. VEPs and the visual pathway

The visual system has a complex architecture; it consists of several pathways that convey aspects of what we see—for example, form, movement, shape, color, etc. Until recently, research has mainly been focused on two major pathways: the parvocellular (PC) pathway, originating in the midget retinal ganglion cells (RGCs), and the magnocellular (MC) pathway, originating in the parasol RGCs. According to this classical theory, the MC pathway is involved in the detection of dynamic shapes, motion, and depth, whereas the PC pathway is involved in the detection of spatial contrasts and color information, with a slower propagation than the MC pathway; these pathways are associated with specific functions, conveying the "what" (V1→V3→V4→IT) and "where" (V1→V2→MT→STS/PP) of visual information (Tanaka, 1996, 1997; see also Fig. 2). However, this simple picture has recently been questioned and refined.

The classical model has to be revised for the following reasons. First of all, several new visual field maps have recently been discovered in humans (V3A&B, IPS-0 to 4, LO-1&2, VO1&2), all located at the back of the cortex (occipital area); they are organized in foveal clusters (see Wandell et al., 2007 for a review). The functional significance of these areas remains to be explored. Furthermore, their basic anatomy, comprising lateral, up-, and downstream connections, still needs to be completely investigated in order to link their functional and topographic properties.

In addition to newly discovered visual field maps, one should also include an entire third pathway in the theory: the

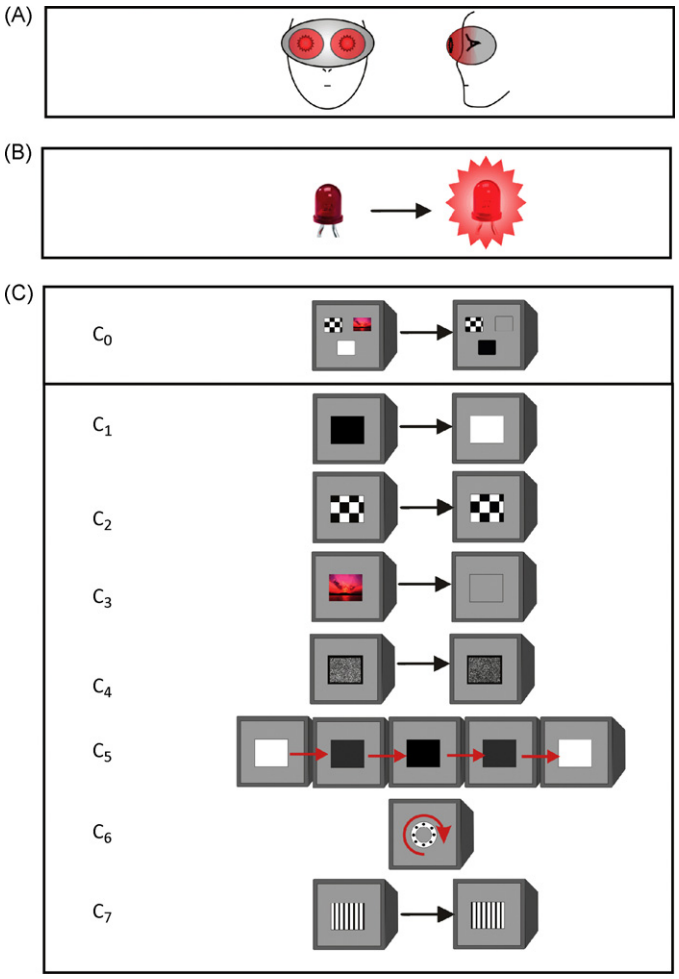

Fig. 1. Examples of stimuli used to elicit transient VEP or SSVEP responses. (a) Flickering light mounted on goggles (usually LCD or LED goggles); (b) light-emitting diode, producing flickering light; and (c) flickering images on a computer screen: (c_0) combination of images that can be used for binocular rivalry paradigms or BCI (see below), (c_1) simple square, (c_2) checkerboard, (c_3) image, (c_4) Gaussian field, (c_5) sinusoidally modulated square, (c_6) rotating or moving stimuli, and (c_7) moving vertical or horizontal gratings.

koniocellular (KC) pathway, originating in the bistratisfied RGCs, must be taken into account as a third independent pathway in nonhuman and human primates (Foxe et al., 2008; Gazzaniga, 2004; Chatterjee and Callaway, 2003; Hendry and Reid, 2000). The complete system consequently has three major parallel pathways, starting from the retina: the MC, PC, and KC streams (Skottun and Skoyles, 2008; Hendry and Reid, 2000; Merigan and Maunsell, 1993; Shapley and Perry, 1986). The three pathways start from the retina, go through the lateral geniculate nuclei (LGN), and finally reach the visual area V1. Functionally, the three pathways originate from cones sensitive to short (S), medium (M), and long (L) wavelengths. This KC pathway is homological to the cat's visual pathway (Szmajda et al., 2006; Hendry and Reid, 2000), where short wavelength (S) cones are associated specifically with the KC pathway and with color perception. This S cone pathway is phylogenetically ancient and present in most mammals (Mollon, 1991). The three pathways hence have specific functional roles (Foxe et al., 2008; Chatterjee and Callaway, 2003; Calkins and Sterling, 1999):

- The MC pathway is achromatic and reacts to low spatial contrast stimuli, especially moving stimuli; it carries depth information. In the retina, it originates from the M and L cones and the parasol RGCs.
- The PC pathway reacts to both high spatial contrast[1] and spectral stimuli (shape and color) and carries the red/green color information. The red/green signal is integrated from the L and M cones by the midget RGCs.
- The KC pathway reacts to spectral stimuli and carries the blue/yellow color information. The blue/yellow signal is integrated from the S cones by the bistratisfied RGCs.

The ventral stream is fed by the KC and PC cells, whereas the dorsal stream is fed by the MC cells (Gazzaniga, 2004). This seems at present the most likely scenario; however, as these functional roles are still being debated, this recent theory might again evolve in the near future to incorporate new discoveries and observations. Note also that the retinal connectivity of the S, L, and M cones with the RGCs is unlikely to be as specific as this theoretical model might suggest (Chatterjee and Callaway, 2002; Lee, 2008).

According to an alternative theory, the KC pathway carries all color information, while the PC pathway only carries fine-resolution spatial information (Calkins and Sterling, 1999). However, this theory does not seem to be supported by sufficient evidence (Foxe et al., 2008; Chatterjee and Callaway, 2003).

The three pathways play a key role in the formation of VEPs at the cortical level. Identifying the role of these three pathways in the formation of both transient and steady-state VEPs is consequently crucial; yet, apparently this problem has not received the attention it deserves. The contribution of PC and MC pathways can be triggered depending on the stimulus; isoluminant chromatic red/green signals preferably stimulate the PC pathway,[2] whereas 100% luminance contrast signals stimulate both the PC and MC pathways (Foxe et al., 2008). Consequently, one stimulates the KC pathway with isoluminant chromatic blue/yellow signals.[2]

An alternative approach was suggested by McKeefry et al.; the PC pathway, assumed to correspond to tonic cells, generates the first harmonic response (in addition to some contributions to the second harmonic), whereas the MC pathway, assumed to correspond to phasic cells, only contributes to the second harmonic response (McKeefry et al., 1996). According to that theory, a selective measure of MC activity may be obtained by focusing on the second harmonic response in pattern ON–OFF VEPs. This approach, however, is not sufficiently supported by empirical evidence (Skottun and Skoyles, 2007).

Consequently, second harmonic responses in VEPs should only be used with caution, if at all, to assess magnocellular activity. For instance, this second harmonic criterion was used in recent studies to identify MC activity in SSVEPs (Johansson and Jakobson, 2006) and VEPs (Kinsey et al., 2006) but with counterphase-modulated stimuli instead of pattern ON–OFF VEPs. This use is out of the scope of the second harmonic method of McKeefry et al. (1996), since the latter is based on pattern ON–OFF VEPs (Skottun and Skoyles, 2007).

1.3. Definitions: transient VEP vs. SSVEP

VEPs elicited by brief stimuli are usually transient[3] responses of the visual system. Transient evoked potentials are responses of the system under study to sudden changes (jumps or steps) in the input (Başar et al., 1999). About 40 years ago, Regan (1966a)

[1] The P cells are not sensitive to spatial contrast levels below 8% (contrary to M cells).

[2] Foxe et al. studied only the PC and MC pathways; the specificity of the KC pathway to blue/yellow colors is our deduction.

[3] Unstable and/or time-evolving responses.

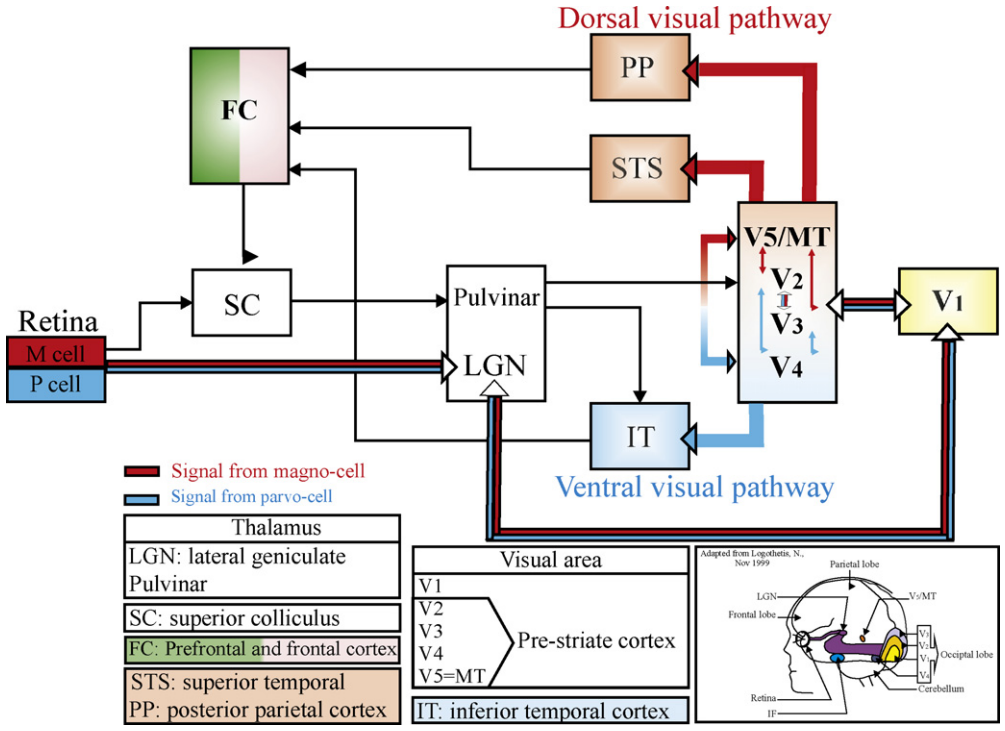

Fig. 2. Simplified illustration of the classical visual pathway. After stimulation of the retina, magno- and parvocell signals are conveyed through the lateral geniculate to the visual cortex (starting from V_1), and next they propagate to other brain areas.

started experimenting with long stimulus trains, consisting of sinusoidally modulated monochromatic light. These stimuli produced a stable VEP of small amplitude, which could be extracted by averaging over multiple trials. These EEG waves were termed as "steady-state" visually evoked potentials (SSVEPs) of the human visual system. SSVEPs can be found in animal models as well (*e.g.*, in primates, Nakayama and Mackeben, 1982; or in cats, Rager and Singer, 1998).

Transient VEPs are useful to determine the time that it takes for a visual stimulus to travel from the eye to the occipital cortex. This measure can be used for diagnostics in ophthalmology and for some clinical applications (such as multiple sclerosis). They can also have useful applications for the study of the brain's visual functional areas (see Wandell et al., 2007 for a review). According to the original definition, steady-state potentials are to be distinguished from transient potentials, because their constituent discrete frequency components remain closely constant in amplitude and phase over a long time period (Regan, 1989). This "constant" characteristic is not a time-domain observation. What remain constant is the spectral distribution (in the frequency domain), not the raw EEG amplitude in time domain[4]: SSVEP contain stationary periodic oscillations. Consequently, the amplitude distribution of the spectral content of SSVEP, with characteristic SSVEP peaks, remains stable over time. Because these characteristics are constant, many applications can be derived from SSVEP propagation properties. A first difference between these two evoked responses is thus their range of application.

In addition, SSVEPs are less susceptible to artifacts produced by blink and eye movements (Perlstein et al., 2003) and to electromyographic noise contamination (Gray et al., 2003). Transient VEPs are typically only used for studying the visual system, whereas the range of applications of SSVEPs is wider—from cognitive neuroscience (see Section 1.7) and clinical neuroscience (see Section 1.8) to neuro-engineering applications with BCI (see Section 2).

For the sake of clarity, we will now illustrate the difference between transient VEPs and SSVEPs (Fig. 3). The shape of the response in time domain usually is not sufficient to distinguish SSVEPs from transient VEPs; instead, spectral response in the frequency domain is critical. The transient response is a complex resonance response to a stimulus. When the stimulus is repeated, this complex response should correspondingly be repeated; this combined response may become organized (with stationary periodic oscillations) or disorganized (without stationary periodic oscillations), and therein lies the difference between transient VEPs and SSVEPs. If the response is organized, the evoked potential may contain periodic components with observable peaks in the frequency spectrum (F2 in Fig. 3); across the repetitive flickering stimuli, the spectrum content of the signal will remain almost the same (it will contain the same harmonic peaks, in phase relation with the stimulus). In addition, the average phase-lag of SSVEP will be proportional to the stimulus frequency. The statistical significance of these spectral characteristics can be assessed using the Victor–Mast statistic (Victor and Mast, 1991; Carney et al., 2008; Appelbaum and Norcia, 2009) to control the significance of SSVEP peaks. In addition, these SSVEP peaks can be enhanced for visualization by applying a filter to the Fourier representation, the "SSVEP signal-to-noise ratio":

$$SNR(f) = \frac{nF(f)}{\sum_{k=s}^{n/2} F(f + k\Delta f) + \sum_{k=s}^{n/2} F(f - k\Delta f)}, \quad (1)$$

where f is frequency, F is the Fourier power of the signal, and Δf is the Fourier transform precision (or frequency step).

In contrast, if the response is disorganized, the phase and amplitude of the frequency components will vary; the frequency spectrum will have no distinct stationary SSVEP components (F1 in Fig. 3). This means that the presence or absence of SSVEP can be estimated only from the spectral characteristics of the signal

[4] The SSVEP signal itself slightly fluctuates in amplitude in the time domain—especially, SSVEP amplitude tends to decrease after the first few oscillations.

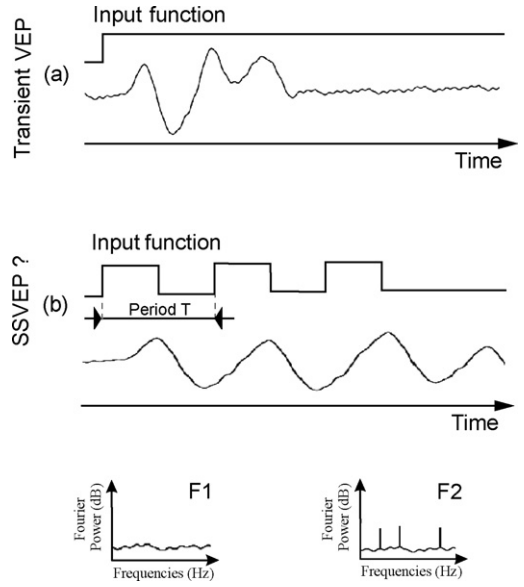

Fig. 3. Transient VEP vs. SSVEP—synthetic model. (a) The upper diagram represents the input function, with a square stimulation (transient); the bottom trace is a transient VEP. (b) The upper diagram represents the input function, a periodic square wave (period T); the bottom trace is either a transient VEP or an SSVEP. If the corresponding Fourier representation does not show a stationary distinct spectrum (as in F1), the response is a transient VEP. If it instead has distinct peaks at the stimulus frequency and its harmonics (as in F2; a square wave elicits responses at the even harmonics), the response is an SSVEP. Note that distinct peaks can only be observed if the Fourier spectrum is calculated over a sufficiently large window ($>T$). If the window is too short, the SSVEP cannot be observed. For example, for a 1 Hz SSVEP, the recording duration must be at least 1 s (see *e.g.* Regan and Regan, 1988). In our example, one may successfully use a window of length $\geq T$. However, if a window of length $<T$ is used, the Fourier spectrum of the SSVEP would not resemble F2 but F1, and as a consequence, an SSVEP could not be observed.

(especially in low frequencies, see also Regan and Regan, 1988). In the case of SSVEPs, the system attains a dynamic steady-state throughout the duration of the recording period without ever returning to its resting state, while for transient VEPs the system returns to its resting state after any given brief stimulus (Regan and Regan, 2005). Note that a sufficiently large window should be used to compute the Fourier representation (Fig. 3).

1.4. Experiments: transient VEP vs. SSVEP

We pointed out earlier that according to Regan's theory (Regan, 1989), initial transients due to adaptation or resonant-like properties of the visual system disappear from SSVEPs after sufficiently long stimulation. As a result, SSVEPs can be relatively easily quantified and reproduced; in contrast, it is hard to describe, quantify, and reproduce transient VEPs (Regan, 1982). Because the Fourier spectrum of SSVEPs shows stationary distinct patterns, basic Fourier power measures can confirm the presence of SSVEPs (see Fig. 4). Moreover, averaging the evoked potentials across trials leads to periodic signals (not necessarily sinusoidal, due to the harmonics; see Section 1.6). More sophisticated signal processing techniques, in particular wavelet representations, enable us to visualize SSVEPs in the time–frequency plane (Fig. 4; Fawcett et al., 2004; Moratti et al., 2007; Weiderpass et al., 2008; Vialatte et al., 2009b).

SSVEPs can be elicited by several types of visual stimuli (Fig. 1). The underlying idea is always the same: a blinking or moving visual stimulus at a constant frequency (the stimulus frequency) elicits a response in the brain at the same frequency and its even harmonics (SSVEP frequency = stimulus frequency plus its even harmonics). Note that this behavior denotes a nonlinearity of the visual system: the Fourier transform of a square wave contains odd harmonics, but its transformation by the visual system contains even harmonics instead.We list some different kinds of stimuli:

- flickering light-emitting diodes (Fig. 1b),
- flickering light (Fig. 1c$_1$),
- alternately inverting bicolor checkerboards (black and white or colored checks, Regan, 1966b, Fig. 1c$_2$),
- flickering image (Fig. 1c$_3$),
- flickering Gaussian noise (Fig. 1c$_4$),
- flickering light with sinusoidal gradation (Fig. 1c$_5$),
- flickering and rotating circles (Fig. 1c$_6$),
- moving gratings (Fig. 1c$_7$).

Yet another type of VEP is the steady-state motion visually evoked potential (Heinrich and Bach, 2003); it is based on a somewhat different principle and will not be studied in detail in this review. The different stimuli in the list above can evoke different responses in the visual system (Spekreijse et al., 1977), depending on their characteristics. As explained in detail in Section 1.2, the MC pathway responds preferentially to stimuli that are color-neutral with diffuse luminance, have low contrast and large grid size, and reverse contrast at a fast rate; the PC and KC pathways respond preferentially to stimuli that contain different colors, have high contrast and small grid size, exhibit significant spatial variation in luminance, and reverse contrast at a slow rate. Therefore, black and white checkerboards at high temporal and low spatial frequencies elicit SSVEPs preferably in the MC pathway; in contrast, color checkerboards with low temporal and high spatial frequencies stimulate the PC (red/green colors) and KC (blue/yellow) pathways more than the MC pathway (see *e.g.* Liu et al., 2006; the KC pathway is not mentioned in that study). The PC and KC pathways are stimulated preferentially by structured stimuli (e.g., checkerboard); they are mostly activated by the low-frequency components. The MC pathway is elicited preferentially by flickering unstructured visual stimuli (e.g., white squares) in the low, medium, and high-frequency ranges (Silberstein, 1995; Vialatte et al., 2009b). This may explain why checkerboard stimuli do not yield strong responses at frequencies above 8 Hz, whereas unstructured stimuli do (Regan, 1978).

Some scientists define the boundaries of SSVEPs in the 3–50 Hz range (*e.g.* Odom et al., 2004). However, this definition is problematic for two reasons. First, flickering stimuli at very low frequencies ($\ll$3 Hz) can elicit SSVEPs[5] (e.g., Regan and Regan, 1988; Herrmann, 2001; Krolak-Salmon et al., 2003; Vialatte et al., 2009a). Second, recent investigations have shown that SSVEPs and SSVEP harmonics can be generated up to 80 Hz; this challenges the upper boundary of SSVEPs (Herrmann, 2001; Birca et al., 2008; Asano et al., 2009). These reports are in line with a theory that relates VEPs to phase resetting (Fig. 5). According to that theory, SSVEPs are not generated by amplitude modulation; instead, they are primarily due to phase alignment of the ongoing background EEG (Moratti et al., 2007): constant rhythmic stimulation induces a reset of the EEG phase, and as a consequence, the averaging of several trials reveals an evoked potential at the stimulus frequency. If this theory is valid, the SSVEP frequency range is limited by the KC, PC, or MC pathway, depending on the stimulus type.

It is possible to give a general definition of SSVEPs, independent of the mechanism that generates them:

Definition: SSVEPs are evoked responses induced by flickering visual stimuli. SSVEPs are periodic, with a stationary distinct spectrum showing characteristic SSVEPs peaks, stable over time.

[5] The low-frequency behavior of any given type of SSVEP may be discovered through experiments, provided that one computes the Fourier (or time–frequency transform) over sufficiently long time windows (or time resolutions).

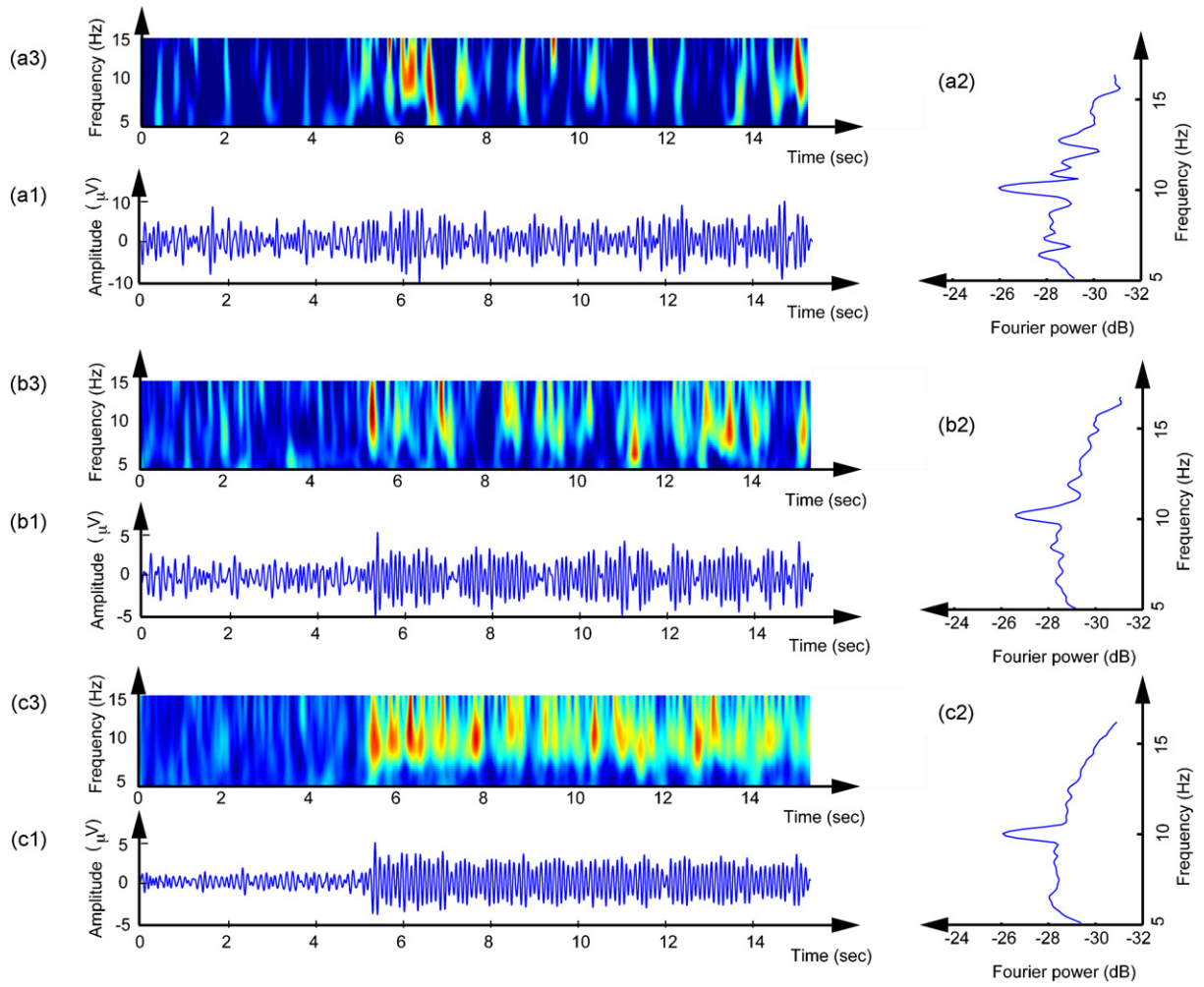

Fig. 4. Example of an SSVEP, elicited by a white square that flickers at 10 Hz (ON–OFF, simple stimulus without pattern): (a) single trial, (b) 10-trial average, (c) 20-trial average. The SSVEP is represented in time (a1, b2, c1), frequency (a2, b2, c2), and time–frequency (a3, b3, c3) domains. Frequency (Fourier) representation is computed with the Welch periodogram method, with windows of 400 ms (=4 cycles at 10 Hz). Time–frequency representation is obtained with continuous complex Morlet wavelets. The semi-stable aspect of this average curve (clearly observable on the time–frequency representation) emphasizes that frequency components of SSVEPs are only *nearly* stationary; averaging more trials yields a more stable curve. The SSVEP is furthermore not a pure sinusoid, due to its harmonics (see Fig. 7).

SSVEPs are better observed in the frequency or time–frequency domains.

Most of the past research on SSVEPs focused on single-frequency stimulation; it is natural to first investigate single-frequency stimulation before considering more complicated stimulation procedures. However, it is known (Regan, 1989) that the combination of two sine waves flickering at frequencies f_1 and f_2 produces a response at the average frequency, $[f_1 + f_2]/2$, together with responses at f_1 and f_2. Recently, more detailed investigations of such combined stimuli have been conducted. For example, one study (Cheng et al., 2001) considered a blinking square, generated by combining red and green light, with distinct flickering frequencies for red and green; it was shown that such a stimulus induced a phase coupling between the two frequency components in the recorded SSVEP. Similarly, a pattern consisting of two stimuli, flickering at two different frequencies, induced a spectral response with peaks at the individual frequencies, in addition to peaks at other frequencies; the latter peaks were caused by quadratic coupling between the two stimulus frequencies and their harmonics (Srihari Mukesh et al., 2006). The exact mechanism underlying this coupling process is at present unknown; moreover, more complex schemes – those with more than two frequencies or with signals that stimulate different pathways; i.e., PC, KC, or MC – have not yet been considered.

SSVEPs can be recorded in various ways: invasive recordings (local field potential, EcoG), scalp recordings (EEG and MEG), and imaging (fMRI, PET, SPECT). SSVEPs may also be recorded directly at the retinal level; they appear in electroretinograms (Tagliati et al., 1996). Successful recordings of SSVEPs with near-infrared spectroscopy (NIRS) have not been reported yet. The fast optical signal obtained with NIRS has been investigated under somato-sensory and visual repetitive stimulation; however, no steady-state potential seemed to occur in any of these modalities (Steinbrink et al., 2005). More investigations should be performed in order to confirm or reject this experimental finding. EEG has often been used to investigate SSVEPs due to its good time resolution and low cost.

1.5. Sources of SSVEPs: experiments and theories

In this section, we describe brain areas that generate SSVEPs. Table 1 gives a general overview of recent dipole or source localization reports. Medium- and high-frequency components in SSVEPs have been attributed to two different but potentially overlapping visual cortex sources, located primarily in V1 (Van Dijk and Spekreijse, 1990). Conversely, low-frequency components of SSVEPs may be generated not only by cortical regions (Spekreijse et al., 1977). On the ground of topographical distribution, several

Table 1
Source location of SSVEPs in recent publications.

Authors	Stimulus	Frequencies	Method	Location(s)
Krolak-Salmon et al. (2003)	Chkb	1.1 Hz, 75 Hz	Implanted electrodes (human subjects)	LGN, V1, V2
Pastor et al. (2003)	Strobe	5–60 Hz (EEG) 5–40 Hz (PET)	EEG + PET	V1[a], cerebellum
Fawcett et al. (2004)	Chkb	1–21 Hz (square) 1–17 Hz (sine)	MEG	V1, V5, MT
Sammer et al. (2005)	Comp	4.7 and 18.8 Hz	Simultaneous EEG + fMRI	Occipital
Zhang et al. (2006)	Comp[b]	26–33 Hz	EEG	V1
Srinivasan et al. (2006)	Dots	3–30 Hz	QEEG + Laplacian	Occipital, parietal, and frontal[c]
Srinivasan et al. (2007)	Chkb	3–14 Hz	fMRI	V1, V2, BA
Di Russo et al. (2007)	Gabor gratings	12 Hz	EEG + fMRI	V1, V5, +(possibly)V3A, V4/V8
Pastor et al. (2007)	Strobe	5–40 Hz	EEG + PET	Frontal eye-fields, Parieto-occipital[a]

Chkb, Strobe, Comp, and Dots = flickering checkerboard, strobe lamp, flickering whole computer screen, and flickering random dot pattern, respectively.
[a] The authors suggest that V1 is not the only area involved in SSVEP generation. In Pastor et al. (2007), the SSVEP harmonics, studied separately, correspond to different sources.
[b] This experiment used the binocular rivalry paradigm.
[c] Occipital and parietal sources are local, whereas frontal sources are either deep or broadly distributed for most frequencies.

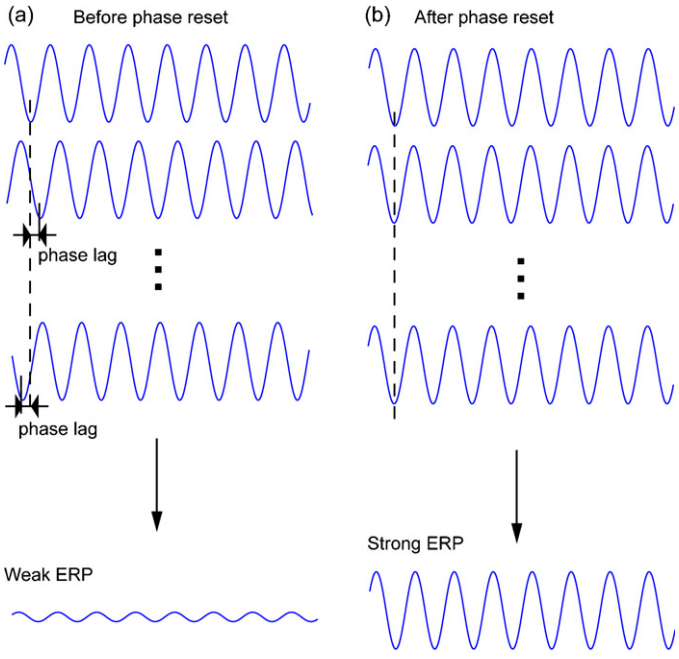

Fig. 5. Phase reset theoretical ERP model. (a) When EEG epochs are not phase-aligned, their average contains only weak event-related potentials (ERPs). (b) When the phases of EEG epochs are precisely phase-aligned, a strong ERP is observed (even if the amplitude in single trials is weak).

authors have suggested that low-frequency SSVEPs originate in subcortical structures, at the retinal level or in fiber tracts. Recently, an early low-frequency SSVEP response was observed in the LGN, recorded by implanted electrodes in a human patient[6] (Krolak-Salmon et al., 2003). This confirms that low-frequency SSVEPs originate prior to cortical areas.

Most recent studies on low-frequency visual stimulation, however, have investigated SSVEPs in the cortex only (4.7 Hz in Sammer et al., 2005; 3 Hz in Srinivasan et al., 2006; 12 Hz in Di Russo et al., 2007; and 3–14 Hz in Srinivasan et al., 2007). To the best of our knowledge, only one brain imaging study of SSVEP sources (PET in particular) reported extracortical SSVEP sources of activation—more specifically, in the cerebellum (Pastor et al., 2003).

According to most studies (see Table 1), the occipital area of the cortex generates SSVEPs. As we already have pointed out, extracortical areas also seem to be involved. Moreover, different parts of the cortex besides the occipital area may play an important role in the generation of SSVEPs: a recent fMRI study reported 3–5-Hz SSVEPs in the medial frontal cortex as well (BA11, BA10). Therefore, SSVEPs seem to occur in a large-scale functional occipitofrontal cortical network, which may be functionally connected to certain extracortical structures (Srinivasan et al., 2007).

It is important to realize that results obtained with different recording and imaging methods should be compared with great care. EEG has good time resolution, whereas PET and fMRI have poor time resolution but much better spatial resolution. Therefore, it is more reliable to compare the results obtained with fMRI or PET with low-resolution tomography[7] (Zhang et al., 2006; Pastor et al., 2007), which should provide more comparable results than other source estimation techniques (because it will extract locally distributed dipoles, similar to those observed with fMRI or PET).

In summary, the only general consensus among these different studies is that the strongest local source of SSVEPs is located in the striate cortex (V1), but this source does not seem to be entirely responsible for SSVEP generation (Pastor et al., 2003; Srinivasan et al., 2007).

Three theories have been put forward to explain the complexity of SSVEP distribution:

(a) First, one may distinguish locally and broadly distributed sources (Srinivasan et al., 2006); the latter sources may account for the wide scalp distribution of SSVEPs observed in EEGs (Fig. 6).

Theory 1: SSVEPs originate in the primary visual cortex and propagate by the combined activity of locally and broadly distributed sources.

(b) Second, it has been suggested that topographical aspects of SSVEPs (power and phase) could be explained by isolated dipoles that are activated sequentially in time (Di Russo et al., 2007).

Theory 2: SSVEPs are generated by a finite number of electrical dipoles that are activated sequentially in time, starting with a dipole located in V_1.

(c) However, while isolated dipoles account for the strongest activity, they may not sufficiently describe the complex distribution of electrical activity in the brain (Thorpe et al.,

[6] This study investigated three human patients suffering from drug-refractory epilepsy but without photosensitivity. Electrodes were implanted for presurgical evaluation.

[7] Brain tomography = imaging by sections, or sectioning, of brain activity.

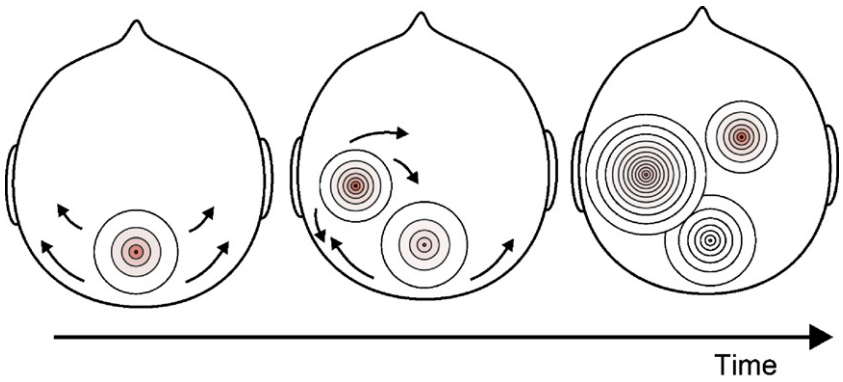

Fig. 6. SSVEP propagation by the combination of locally and broadly distributed sources. The concentric circles with red colors represent dipoles, and the arrows their propagation. (Left) Preliminary local activities in primary visual areas, observable with PET/fMRI, start propagating; (center) the activity propagation, in turn, activates secondary broad sources (observable with EEG); (right) VEP reaches its steady-state with a succession of local and broad dipoles. These dipoles depend on stimuli characteristics, which explains the complex patterns observed in EEG topography.

2007). This distribution may be explained by a traveling wave model (e.g., see Burkitt et al., 2000), in which cortical traveling and standing waves may propagate from visual areas to nonvisual areas in the cortex (Silberstein, 1995).

Theory 3: VEPs originate in the primary visual cortex, and propagate to other brain areas through cortical and standing wave.

These theories only have in common the fact that SSVEPs propagate, starting from the primary visual cortex, and involve more than one single source dipole; the single dipole source in the occipital lobe is inadequate to explain the dynamic spatial patterns of SSVEP magnitude and phase (Thorpe et al., 2007). Theory 3 is more specific for the EEG phenomenon and does not account well for fMRI/PET observations. Theory 2 is more specific for the fMRI/PET phenomenon and does not account for the wide variety of topographies observed in EEG. Theory 1 seeks to integrate both EEG and fMRI/PET observations. Consequently, these three theories are not necessarily contradictory—they correspond to different perspectives.

Theory 1 has an advantage and a better explanatory power regarding all of the available data; it bridges the gap between the differences in scale of EEG and fMRI/PET (Fig. 6). Note, however, that this theory introduces a distinction between long-distance and local brain dynamics, which is a usual aspect of EEG models, but is not classical for fMRI/PET models. Consequently, further evidence will be necessary to confirm this theory.

1.6. SSVEP components

Despite years of investigation, the complex mechanisms behind SSVEPs are not yet fully understood. One usually distinguishes three different components in SSVEPs (Spekreijse et al., 1977; Regan, 1989; Silberstein, 1995; see Fig. 7, top):

- A primary component in the high-frequency range (gamma 25–60 Hz range), with small interindividual variability, and typical latency of about 30–60 ms. Early responses at 10 ms have been reported, however, and the latency of this component seems to increase progressively with age.
- A secondary component in the 15–25 Hz range, with higher interindividual variability and latency of about 85–120 ms.
- A rhythmic after-discharge below 15 Hz, with a latency of 135–350 ms (on average 250 ms); this component takes several cycles to reach its steady-state level after the start of stimulation and does not immediately stop when the stimulus is switched off.

Different topographies have been observed for each component, and the phase topography of SSVEPs shows considerable intersubject variability (Silberstein, 1995). The three components may appear after averaging, but they may be extracted more effectively by Fourier analysis. By selecting the stimulus frequency,

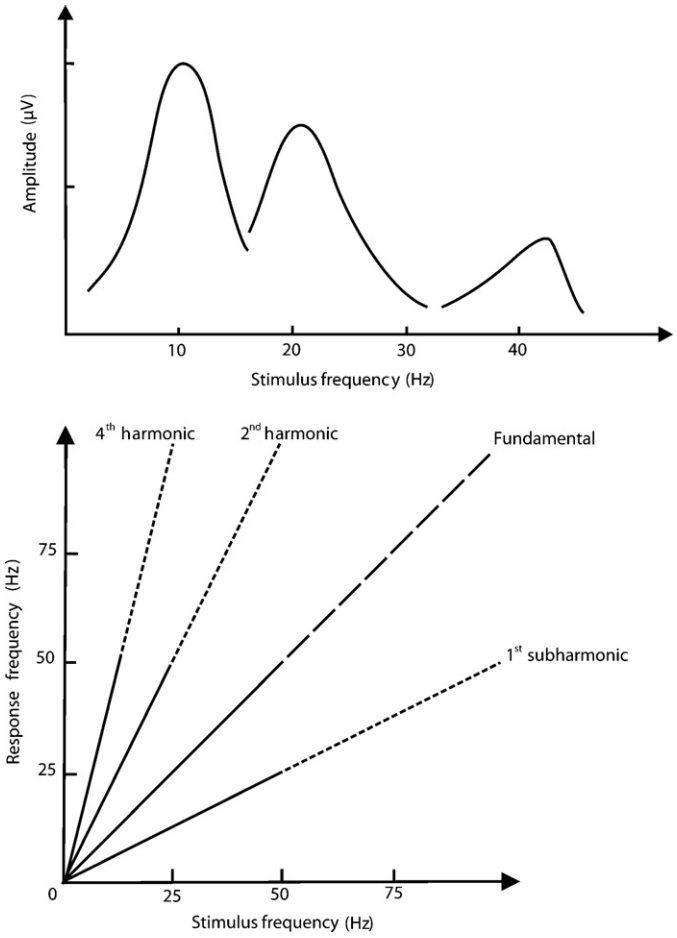

Fig. 7. Synthetic model of the three SSVEP components. Top: each component responds preferentially to low-, medium-, or high-frequency stimulus, with peak responses near 10, 20, and 40 Hz. Bottom: the SSVEP response is recorded at its fundamental and harmonic frequencies (Regan, 1989; Silberstein, 1995; Herrmann, 2001). This model might be extendable up to at least 100 Hz (Herrmann, 2001); there might be also more components yet to be discovered at higher frequencies. Note that this organization shows great intersubject variability.

it is possible to evoke certain SSVEP components more than others, and therefore, one may generate different evoked potentials; the SSVEP contains sinusoids at the fundamental and harmonic frequencies of the stimulus (Fig. 7, bottom).

1.7. Applications in cognitive neuroscience

As we mentioned several times earlier, SSVEP responses have a stable spectrum and high signal-to-noise ratio. As a consequence, SSVEPs are useful tools to study the neural processes underlying brain rhythmic activity (Silberstein, 1995); they have been successfully applied in a wide range of cognitive and clinical investigations. In this section, we will review those studies. In Section 1.7, we consider studies of SSVEPs related to cognition. In Section 1.8, we review applications of SSVEPs to clinical neuroscience. In Section 2, we will focus on yet another application of SSVEP—i.e., brain computer interface (BCI).

In cognitive neuroscience, the SSVEP is often used as a steady-state "topographical probe" (SSTP, Silberstein et al., 1995, 1990); it is used as a frequency tag associated with a visual task.[8] The SSVEP frequency propagation in task *vs.* control states is used to indirectly estimate the propagation of EEG signals related with the task. This method, used mainly in the alpha range, was used to observe correlates of cognitive processes, mainly in the prefrontal cortex (Silberstein et al., 2003). The SSTP topographic distribution is stable to changes of SSVEP frequency (Wu and Yao, 2008).

1.7.1. Visual attention

The most well-known cognitive mechanism studied through SSVEPs is visual attention (Morgan et al., 1996). Visually evoked responses are substantially enhanced if the flickering visual stimuli fall within the area of spatial attention. This effect is more prominent in the right frontal hemisphere[9] than in the left one; however, this hemispheric asymmetry disappears after long presentation of the stimuli (Keil et al., 2005). When intermingled red and blue dots are displayed, flickering at different frequencies, subjects focusing their attention on either blue or red dots have increased SSVEP amplitudes for the attended stimuli (Müller et al., 2006). SSVEP amplitude was also successfully used as a predictive feature for attention fluctuation in an RSVP[10] study. This effect was observed using both emotionally arousing stimuli (Keil et al., 2006) and neutral German words as targets (Keil and Heim, 2009).

Attention can also be investigated using SSTPs. The idea is to use SSVEPs as "frequency tags" in order to study the temporal characteristics of visual spatial attention (Müller, 1998); the propagation of the SSVEP peak frequency from the primary visual areas into different brain areas is used to track the neural dynamics correlated with the attention task. SSTPs can also be used to investigate attention and emotional responses to pictures. Pictures with emotional contents, flickering at 13 Hz (Kemp et al., 2002) or 10 Hz (Keil et al., 2005), were successfully used to estimate the timing and amplitude of cortical responses to affective stimuli. Differences in SSVEP phase showed correlates of arousal, and SSVEP responses had reduced latency when affectively arousing stimuli were attended. SSVEP frontal amplitude was decreased for images of unpleasant valence (Kemp et al., 2002). However, increased occipito-temporal and parietal activations were observed for combined higher spatial attention loads and emotional contents (Keil et al., 2005).

[8] Note that this method is effective when the SSVEP is in a frequency range related with the task under investigation.

[9] There is much evidence that the right hemisphere plays a predominant role in spatial attention.

[10] RSVP = rapid serial visual presentation. In this experimental paradigm, several stimuli are displayed quickly together with distractor items, while the subject is requested to identify relevant information.

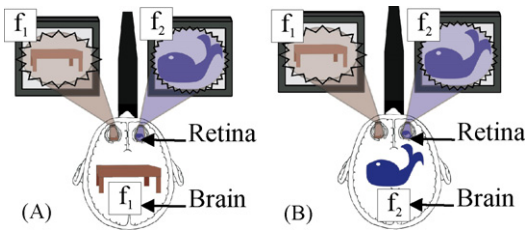

Fig. 8. Binocular rivalry SSVEP paradigm. Flickering targets at differing frequencies are projected onto each visual hemifield. Subjects will usually perceive only one of the two rival stimuli, the perception switching from one stimulus to the other; an SSVEP is generated at the frequency of the perceived stimulus. The subjectively perceived stimulus and the excited brain areas may therefore be objectively determined from the EEG signals simply by extracting the SSVEP. In the above example, target 1 is a table image associated with a frequency f_1, while target 2 is a whale image associated with a frequency f_2. In condition a, the subject perceives the table, and a peak at frequency f_1 may be detected in the EEG. Conversely, in condition b, a peak at frequency f_1 may be observed in the EEG when the subject perceives the whale.

1.7.2. Binocular rivalry

Another well-known paradigm used for the investigation of conscious visual perception is binocular rivalry; two incongruent visual targets are simultaneously presented—one target in one visual hemifield, the second target in the other hemifield. Unfortunately, binocular rivalry is a very subjective phenomenon; only the subject knows when he switches his perception. However, it was shown that the attended target can be identified with SSVEP paradigms: for instance, if the two targets are LED flickering at different frequencies, the amplitude of the SSVEP response to the attended target is enhanced (Müller et al., 1998). This is the reason why it was suggested that binocular rivalry could be advantageously combined with SSVEPs; the two targets flicker at two different frequencies, and SSVEPs are generated at the frequency of the subjectively perceived target (see for instance Wang et al., 2005a,b; Srinivasan and Petrovic, 2005; Sutoyo and Srinivasan, 2009) (Fig. 8).

1.7.3. Working memory

Working memory (WM) refers to temporarily storing and manipulating cognitive information, such as mental representations. This memory has a dynamic nature (contrary to long-term memory, its content evolves quickly). In order to understand the mechanisms of WM, one needs to uncover its different phases and corresponding neural correlates. In this context, SSVEPs are used as frequency tags; because SSTP responses propagate through the brain, the memory load can be estimated from the decrease of SSVEP amplitude. Studies on working memory demonstrate the usefulness of SSTPs (Silberstein et al., 1995, 1990), especially in the alpha range, which is one of the possible correlates of WM.

For instance, Perlstein et al. (2003) measured the SSVEP responses to a 10 Hz diffuse background flicker during the performance of a visual delayed response WM task, in which subjects had to remember images during 8.2 s. During this flickering stimulation, EEG tomographic measurements of the alpha band decreased when the subject performed the WM task, an observation buttressed by fMRI observations (Perlstein et al., 2003). This demonstrates that SSTPs are sensitive to WM demand. A 13 Hz SSVEP was also used as a frequency tag during a Shepard and Metzler mental rotation task (Silberstein et al., 2003). During flickering stimulation, the mental rotation task complexity was associated with an increase in fronto-parietal synchrony (as measured by partial coherence). More recently, similar effects of WM load on a 13 Hz SSVEP were also seen in the context of an n-back task (Ellis et al., 2006), in which the subjects had to remember the position of dots at specific times in a series of images (1, 2, or 3 images before).

Frontal area responses (Fourier power) were decreased with increasing complexity of the task (1-, 2-, or 3-back task). Different SSVEP topographies were found, depending on the period (perception *vs.* storing of memory). From SSTP evolution, the authors hypothesized that the frontal cortex is "loaded" in the early period and "reallocated" to executive aspects of the task in the late period, with a shift of the "holding" content from frontal to occipital regions.

1.7.4. Alpha range

An understanding of the fundamental rhythms of EEGs is important for basic neuroscience. The alpha range (8–12 Hz) activity is easy to observe in EEGs and was the first rhythm investigated. This activity usually increases when eyes are closed in the occipital region and is affected by mental tasks (*e.g.*, see section 1.7.3). Usually, one observes a peak in the alpha range. The location of this peak (usually near 10 Hz) varies according to the age of the subject and can be affected by brain disorders. As we explained earlier, SSVEP peaks at about 10 Hz, in the frequency range. Above 10 Hz, although SSVEPs are still recorded, they become less perceptible for subjects (Regan, 1966a,b)—in other words, there is a disparity between objective measurements and subjective perceptions. It seems logical to validate if the alpha range activity and alpha peak have a causal relationship with the SSVEP peak near 10 Hz in subjective and objective measurements.

A resonance phenomenon at the alpha rhythm's fundamental and harmonic frequencies was observed (Herrmann, 2001); the frequency subsystems of SSVEPs (with peaks at 10, 20, 40, and 80 Hz) could be explained as an alpha range harmonic organization of the brain. The model of frequency subsystem could be extended up to above 75 Hz (but subjects do not perceive the stimulus beyond 75 Hz), with low (10 Hz peak), medium (20 Hz peak), high (40 Hz peak), and very high (80 Hz peak) subsystems. Hermann conjectured that a link between alpha and gamma brain rhythms may exist because of this resonance phenomenon (Herrmann, 2001). It is to be mentioned that previous invasive recordings in cats (Rager and Singer, 1998) did not show this alpha resonance phenomenon; hence, the alpha resonance could be either specific to differences between human or cat models, due to the specific flash VEP used by Herrmann, or due to a flaw in Herrmann's experiment. A counterstudy would be necessary to answer this question.

It was reported (Birca et al., 2006) that the dominant frequency of spontaneous EEGs (the alpha peak, explained above) was first located in the resting condition with the eyes closed. During SSVEP stimulation with the eyes closed (with a photostimulator at 5, 7.5, 10, and 12.5 Hz), the amplitude EEG near this peak is decreased, in correlation with SSVEP amplitude. In other words, during flickering stimulation, the dominant alpha peak is suppressed (or desynchronized). This suppression was specific for the dominant spontaneous EEG frequency of each subject, rather than a certain invariable frequency band across all subjects, with greater suppression of the dominant rhythm at lower compared with higher SSVEP frequencies. This study demonstrates a causal interaction between SSVEPs and spontaneous alpha activity (SSVEPs influence spontaneous activity). Hence, the interaction between spontaneous and evoked activity during SSVEPs is most certainly supported by specific cellular mechanisms, which are yet to be explored (Birca et al., 2006).

These observations demonstrate that SSVEPs can be used to obtain a better understanding of alpha rhythm mechanisms. An understanding of the mechanisms of this fundamental rhythm is important from the perspective of basic neuroscience. Furthermore, it could later on open new avenues of applications for clinical neurophysiology; in the medical context, diseases are understood by comparing physiological *vs*. pathological states. Progress in the understanding of physiological states is consequently helpful for studying pathological states. For instance, 10 Hz flickering stimulation was reported to enhance memory in older subjects (Williams et al., 2006); this is an application for a specific problem (pathological context): aging. However, the possible biological connection between alpha range EEGs and memory (physiological context) is not well documented; consequently, interpreting the result reported by Williams et al. becomes difficult. This clearly emphasizes the link between basic neuroscience and its applications in clinical neuroscience, which we will review in the next section.

1.8. Applications in clinical neuroscience

The application of VEPs as a diagnostic and study tool in clinical neuroscience is not new (see Regan, 1989 for a review). More specifically, SSVEPs have also been used intensively for clinical investigations. In that context, SSVEP stimulation is often referred to as "intermittent photic stimulation," and SSVEPs are labeled as "photic driving." Photic driving is a subclass of SSVEPs, elicited with strobe flashes or photostimulators. In clinical studies, SSVEPs are used to investigate pathological brain dynamics.

1.8.1. Aging and neurodegenerative disorders

SSVEPs can also be used to investigate aging and particular disorders related to aging, such as Alzheimer disease and other dementia. SSVEPs were, for instance, used to show that Alzheimer-demented people seemed to suffer from a dysfunction of the MC pathways (Jacob et al., 2002), using medium and high frequencies of SSVEPs to trigger the MC system (the MC pathway reacts preferably to high frequencies, *see* Section 1.4).

Using SSVEPs, spatiotemporal visual abnormalities were known to occur in Parkinson disease (Marx et al., 1986), related to retinal dopaminergic deficiency (e.g., Stanzione et al., 1986). Pattern electroretinograms were shown to retrieve retinal steady-state responses efficiently and can be used for clinical assessment and monitoring of dopaminergic therapy in Parkinson disease (Tagliati et al., 1996).

Memory degrades with aging. Two memory tasks were compared using an SSVEP paradigm: object working memory and contextual recognition memory (Macpherson et al., 2009). SSVEP amplitude and latency were used as a marker of neural activity. For object working memory, older adults demonstrate reduced neural activity, whereas for contextual recognition memory, neural activity is increased. These effects are attributed by the authors to a compensatory mechanism depending on the memory task complexity. For healthy elderly people, alpha frequency (9–11.5 Hz) flickering stimuli also have been shown to facilitate episodic memory (explicit memory of autobiographical events) (Williams et al., 2006); subjects performed better at an episodic memory task after SSVEP stimulation than before. The authors hypothesized that SSVEP activity may increase the "gain" within recurrent cortico-cortical and cortico-thalamic loops (in other words, SSVEPs stimulate the alpha range oscillations). This theory represents hope for sufferers of brain disorders affecting episodic memory; however, this experiment was not reproduced until now, and the theory does not have solid evidence yet.

1.8.2. Schizophrenia

EEG activity of patients with schizophrenia is different from normal subjects, both at rest and during stimulus processing. Because of their greater stability, SSVEPs can provide precise insights into the neural dynamics of schizophrenia. It is well established that schizophrenic patients usually have smaller SSVEP amplitudes (Clementz et al., 2004; Krishnan et al., 2005). However, during photic stimulation at 1–30 Hz, the visual cortex of schizophrenia patients seems to be more activated compared to

control subjects; this phenomenon was observed through fMRI (Renshaw et al., 1994) and PET imaging (Taylor et al., 1997). With small SSVEP amplitudes, this increased blood flow could be interpreted as a compensatory mechanism. This increased blood flow during visual stimulation in schizophrenia patients may consequently be attributed to:

(a) An anomaly in the retinal response, propagating an abnormal signal to the visual areas; and
(b) The inability of the visual neural circuits to synchronize to periodic external stimuli.

The visual system of a schizophrenic patient has a dysfunction specific to the MC. Using structured and simple SSVEP stimuli to activate the PC or MC pathway system preferentially (see Sections 1.2 and 1.4), a reduced activation of the MC visual system was observed (Butler et al., 2001; Kim et al., 2005, 2006). This anomaly is significantly correlated with cognitive deficits in motion processing in schizophrenia (Kim et al., 2006). A biological mechanism at the retinal level is consequently (at least partly) responsible for the abnormal SSVEP latency in schizophrenics (hypothesis 'a'). Note that this observation is not necessarily contradictory with poor coordination between distant cortical regions (hypothesis 'b').

Finally, SSVEP latency is delayed for schizophrenic patients during simple SSVEP stimulation (Clementz et al., 2004). If combined with a visual vigilance task (Silberstein et al., 2000), this latency increase is correlated with patients' reaction times. Furthermore, the second prior to auditory hallucination, the latency is significantly decreased (Line et al., 1998). This abnormal SSVEP latency might consequently be correlated with the pathology mechanism.

1.8.3. Ophthalmic pathologies

Visual acuity[11] of infants and children can be evaluated by measuring VEP responses. Pathologies of visual acuity are attributed to sensory (neuronal) or optical (ophthalmic) deficits. In this context, one can benefit from the stability of SSVEPs, whose characteristics can be used as markers for pathologies. In Down syndrome, infants and children show reduced visual acuity and contrast sensitivity when compared to other children. SSVEPs and behavioral techniques have shown that this visual deficit is purely sensory (John et al., 2004) by measuring the visual acuity of children with the syndrome but without ophthalmic anomalies.

Asthenopia is an ophthalmological condition with non-specific symptoms, such as eye strain, red eyes, blurred vision, and headache. Subjective reports of pain in children suffering from asthenopia mention that symptoms may be reduced when wearing colored lenses. The lens colors are chosen from subjective feelings and are not consistent between subjects. In other words, this pathology is not associated with a specific color and cannot be attributed to a specific pathway (MC, PC, or KC; see Section 1.2). SSVEP induction at 12 Hz (pattern stimulus) in children wearing colored lenses or not distinguished those who suffered from asthenopia without headaches from those who suffered from visual stress with headaches (Riddell et al., 2006). This showed, for the first time, an objective neurological correlate of the subjective beneficial effects of wearing colored lenses for sufferers of asthenopia.

1.8.4. Migraine

Migraine is poorly understood and is consequently underdiagnosed and undertreated. There are several types of migraines, each with specific symptoms. The most prevalent type of migraine is a throbbing headache, often one-sided. This type of migraine starts locally then spreads and builds up in intensity over the next hour or two, often accompanied by other symptoms (such as nausea, vomiting, and sensitivity to light or sound).

Slowing and asymmetry of the dominant frequency in the alpha range were found during the critical phase of migraine as compared to attack-free periods (de Tommaso et al., 1998). Alpha range activity thus seems to be significantly involved in the brain dynamics of migraine. SSVEP patterns were successfully used as markers of migraine, distinguishing control subjects from migraine patients in attack-free periods (de Tommaso et al., 1997; Shibata et al., 2008); and migraine patients with aura[12] from migraine patients without aura (Shibata et al., 2008). Consequently, migraine patients may have an overactive regulatory mechanism, prone to instability (Angelini et al., 2004); normal light becomes unpleasant, normal sound becomes uncomfortable, and normal pulsing of vessels is probably felt as pain. All of these effects are hypothesized to be caused by a dysfunction of the neural mechanisms of synchrony in the brainstem. In migraine patients with aura, alpha band phase synchrony is increased during 17–24 Hz SSVEP (flash stimuli) as compared to healthy subjects (Angelini et al., 2004)—this effect was however not observed at 5 or 10 Hz (Shibata et al., 2008).

1.8.5. Depression

Depression is regarded as an affective disorder, with disturbed processing of emotional information. The principles of SSTPs (see Section 1.7) can be applied to studies of neural correlates of emotions using flickering emotional pictures (attracting the subject's attention) or pictures with different valences (inducing negative or positive emotions). The pharmacological effect of serotonin was investigated using images of different valences. The electrophysiological correlates of emotional images of different valences were measured before, or after, the administration of a serotonergic antidepressant (a selective serotonin reuptake inhibitor; Kemp et al., 2004). SSTPs were measured with 13 Hz SSVEPs, and response to pleasant valences was potentiated, whereas response to unpleasant valences was suppressed during acute serotonergic augmentation. This result suggests a possible neurophysiological mechanism underlying antidepressant drug action on emotion.

SSVEPs were recently exploited to show that patients suffering from a major depressive disorder had low activation in the right temporo-parietal cortex when watching arousing stimuli, although they had normal occipital activation (Moratti et al., 2008). According to the authors, this result points to deficits in arousal-related brain structures, along with intact basic visual stimuli processing in patients with major depressive disorder.

1.8.6. Autism

Autism is a developmental disorder, variable in expression, which is characterized by impaired social interaction and communication, and by stereotyped and repetitive behavior patterns. Young children and adults with autism often have abnormal reactivity to sensory stimuli: they cannot filter out irrelevant stimuli.

This abnormal perception was tested using a task where normal and autistic adult subjects were required to shift their attention between flashing targets alternating between left and right visual hemifields (Belmonte, 2000). The targets were flash flickers, eliciting an 8.9 Hz SSVEP response. For control subjects, steady-state response increased and background EEG decreased in the brain hemisphere contralateral to the attention shift. When autistic subjects were allowed less than 700 ms to perform the task, steady-state brain electrical response was augmented and

[11] Visual acuity = clearness of vision (especially of shapes).

[12] Some patients can have a sensory disturbance and hallucinations (not necessarily visual) called "aura" before the migraine onset.

background EEG decreased in both hemispheres for rightward shifts as compared with leftward shifts. With longer time delays, persons with autism showed no modulation of background EEG and high variability in steady-state response. In other words, the responses in brain hemispheres did not display the independent modulation observed for normal subjects. This abnormal activity could be a neural correlate of the non-specific mechanism of sensory gating in autistic subjects (Belmonte, 2000).

1.8.7. Anxiety and stress

Anticipatory anxiety is a form of human anxiety related to imminent threat or danger. While being experienced by healthy individuals, it also occurs within a number of clinical anxiety disorders. Anticipative anxiety can be reproduced in the laboratory when a painful stimulus is delivered to a subject, with prior warning (usually nonreliable warnings) and a random time delay. During the period between the warning and the painful stimulus, the subject is expected to feel anxious. SSVEPs were used as a marker to study anticipative anxiety (Gray et al., 2003). While subjects performed a task, if their screen displayed a red border, they knew that they might receive an electric shock. Neither the probability nor the delay between warning and shock was told in advance, so the red border was used as a triggering stimulus of anxiety for electric shocks. SSVEPs were then used as SSTP markers (see Section 1.7.3) of the brain dynamics related to this experimentally induced anxiety. SSVEP latency was significantly altered by anxiety; latency increased within prefrontal and temporal cortical regions and decreased within occipital regions (and amplitude increases). Latency changes were interpreted by the authors to result from alterations in the loop transmission time of local cortico-cortical feedback loops.

1.8.8. Epilepsy

SSVEPs can elicit epileptic responses to luminance or chromatic stimuli. The most famous case happened in Japan during the Pokemon TV show in 1997, where flashing red-blue images induced massive photoepilepsy and photosensible migraines (Radford and Bartholomew, 2001; Zifkin, 2001), with more than 12,000 children displaying signs and symptoms of illness. In the clinical context, photosensitive epilepsy is usually studied using a specific type of SSVEP, termed photic driving, elicited with repeated flash-VEPs (also called intermittent photic stimulation) produced with photostimulators or stroboscopic lamps. While SSVEPs are produced, one looks for signs of epileptiform or hyperphasic waves in the EEG signal. This procedure is questionable (Ahmed et al., 2006), as it can induce an epileptic crisis during the test, and other approaches for detection have been investigated that can modernize the procedure—for instance, using low-frequency SSVEPs (2 Hz in Vermeulen et al., 2008).

The epileptic response is sensitive to luminance, with higher luminance inducing a higher risk of epilepsy. While epileptic seizures can be elicited by stimuli starting from 20 cd/m^2 only (see Harding et al., 2005 for review), typical photostimulators can produce flash stimuli with luminance $>$100 cd/m^2 from 1 to 60 Hz (Rubboli et al., 2004). Epileptic responses were reported from 3 Hz and up to 84 Hz but with predominance between 10 and 20 Hz. The chromaticity of the stimulus also has a strong impact on the response effect, and low luminance chromatic stimuli using red colors can induce epileptic responses (Rubboli et al., 2004; note also that the Pokemon accident was with a red/blue pattern). Drew and colleagues showed that red/blue and green/blue flickers had the strongest effect on both pupil contraction and epileptic responses (Drew et al., 2001). Strong responses for chromatic stimuli in low frequency consequently indicate a strong role of the PC (red/green, preference for low frequency) and KC (blue/yellow, probable preference for low frequency) pathways for photosensitive epilepsy. Interestingly, the strongest responses were reported for colors of the PC vs. KC pathways, which was not commented on by the authors. This might indicate a pathogenic interaction of KC and PC in the genesis of photosensitive epilepsy. Unfortunately, red/yellow and blue/yellow stimuli were not tested by Drew et al.

The effects of mono- or bicolor flicker stimuli were compared with normal subjects (Nishifuji et al., 2006). In this study, 10 Hz SSVEPs were recorded in response to different color conditions (red/blue, red/green, and red/yellow) using LED checkerboards. SSVEP responses to red/red stimuli (with strong/weak luminance) were also controlled. Spatial distribution of the amplitude and phase difference changed during red/blue stimuli. This specific distribution supported the hypothesis that epileptic seizures may be generated by a mechanism of long-distance (fronto-occipital) coupling. If this hypothesis is correct, it would also be supportive of the theory of SSVEP propagation through the interaction of locally and broadly distributed sources (Theory 1, in Section 1.5).

Other types of pathologies related with epilepsy are also studied using SSVEPs. A recent study (Birca et al., 2008) showed that SSVEP harmonics in the gamma range (50–100 Hz) have significantly stronger amplitudes and greater phase alignment for patients with febrile seizures. In children with focal epilepsy, a similar effect in the gamma range was shown (Asano et al., 2009) but using SSVEPs in an indirect way: instead of stimulating the gamma activity directly, the stimulus was strobe light flashing at 1 Hz, and the effect was observed across the whole frequency range.

As a conclusion, as we do not know much about the mechanisms of photosensitive epilepsy, it seems surprising that flickering stimuli in our environment are seldom studied. For instance, implanted recordings showed SSVEP effects of a computer refresh rate (Krolak-Salmon et al., 2003). Yet, no one has studied the long-term effects of constant exposure to environmental "flickering noise." From a deontological perspective, let us insist that researchers studying SSVEPs always need to reject subjects with epilepsy and migraines from their studies. Further, they would be well advised to test adverse effects of flickering stimuli before exposing a subject to long-term stimulation of high luminance; photic driving can induce several unpleasant migrainous symptoms (such as occipital seizure, migraine, nausea, headache, and vomiting) in addition to the danger of epileptic seizures (Zifkin, 2001).

1.9. Other steady-state responses

The principle of all steady-state evoked potentials (SSEPs) is generally following a principle somewhat similar to SSVEPs: a steady-state response is recorded, usually in the frequency domain, in response to a repetitive stimulus. We have seen that SSVEPs can be used to study the visual system. SSEPs in vestibular, gustative, and olfactory modalities might be possible to induce; however, taste and smell are usually not transient, and designing a repetitive taste or odor seems difficult, if not impossible. To the best of our knowledge, although evoked responses can be recorded in these systems, SSEP paradigms were never described. A design to evoke SSEPs in the vestibular system seems more feasible; yet, it was never investigated.

In auditory and somatic systems, SSEPs have been documented. We will not review SSEPs in these two sensory modalities in detail. We nevertheless present the key information and references in this section for comparison with SSVEPs.

1.9.1. Auditory steady-state response

During rhythmic stimulation of the auditory pathway, a 40 Hz steady-state response has been recorded in the auditory system

(Galambos et al., 1981; Stapells et al., 1984) and was termed the auditory steady-state response (ASSR). Since then, ASSRs have been investigated considerably (see Plourde, 2006 for review). In order to record ASSRs, an auditory stimulus is presented with repetitive tone bursts, generally produced using sinusoidal amplitude modulation of a continuous tone. A sustained evoked activity is recorded afterward, with peaks at the burst rate frequency and harmonics. ASSRs are stereotyped, with known responses limited to the gamma range only, either at 40 Hz or, more recently, in the 80-100 Hz range (*e.g.*, see Burkard et al., 2006). Furthermore, contrary to SSVEPs, upper harmonic (both even and odd) components are recorded, whereas no subharmonics are observed.

1.9.2. Steady-state somatosensory evoked potentials

Steady-state responses to somatosensory stimulation (SSSEPs or SSMPs) were discovered shortly after SSVEPs (Franzén and Offenloch, 1969; Namerow et al., 1974; Regan, 1989; Snyder, 1992). SSEPs are recorded when repetitive modulated vibrations or electric stimulation is applied to a part of the body (usually the hands). SSMPs can be recorded from 2 to 200 Hz, with a dominant peak at 20 Hz (Regan, 1989; Tobimatsu et al., 1999; Nangini et al., 2006). They display many subharmonics but generally no higher harmonics or only one weak second harmonic (Tobimatsu et al., 1999). Few harmonic distortions are observed above 40 Hz (the SSMPs becomes nearly sinusoidal) (Namerow et al., 1974; Regan, 1989). Although there have been many studies on the visual and auditory SEP, the somatosensory SEPs were nearly neglected by scientific studies until 1999 (Tobimatsu et al., 1999). Despite new applications of SSEPs, as regularly demonstrated in the scientific literature (e.g. Cincotti et al., 2007), very few studies have investigated their basic mechanisms (to the best of our knowledge, since 1999, only Nangini et al., 2006).

2. SSVEPs for BCI

Brain–computer interfaces (BCIs) aim to provide a direct and nonmuscular communication and control channel between the human brain and a computer (Fig. 9); the computer may be connected to various devices that interact with the environment—e.g., motors and activators that control a wheelchair (see Wolpaw et al., 2002 and Allison et al., 2007 for review). BCI systems need to react sufficiently rapidly to human commands, and therefore, the brain signals used as inputs to BCI systems need to have good time resolution; therefore, virtually all BCI systems use electroencephalographic recordings (invasive or noninvasive) as input signals. Over the last 20 years, much exciting progress has been made on BCIs. Brain signal features, such as internally or externally triggered event-related potentials (ERPs) as well as event-related synchronization and desynchronization, can be used to encode various user commands, and therefore, they are often considered as elementary building blocks for BCI systems (Pfurtscheller and Neuper, 2006).

The basic idea of using SSVEPs to drive a BCI system dates back to 30 years ago, when the first ancestor of SSVEP-BCI was depicted in a publication (Regan, 1979). The BCI system that was proposed in that study used closed-loop feedback to control the contrast of a pattern stimulus directly from SSVEP amplitude. The application of SSVEPs to BCIs was introduced later by Cheng and Gao (1999). The BCI system processes noninvasive EEG signals to guide a 2D cursor, and the EEG signals are recorded at occipital brain areas while subjects focus on four flickering squares at different frequencies, each encoding a different command (up/down/right/left); those signals are then processed to move the 2D cursor. The more general idea is to encode user commands in flickering light stimuli that induce SSVEPs at different frequencies; the user selects one of the commands by focusing on one of the flickering stimuli, and by analyzing the generated SSVEP, the BCI system tries to infer which stimulus the user selected (Fig. 10). Along those lines, Middendorf et al. (2000) developed a noninvasive BCI system based on SSVEPs, in which two flickering buttons are displayed on a computer screen and the user can select one of the buttons simply by focusing on one of them. In this section, we will review more recent developments in SSVEP-BCIs for noninvasive EEG (see Table 2). We will also address various technical issues in more detail.

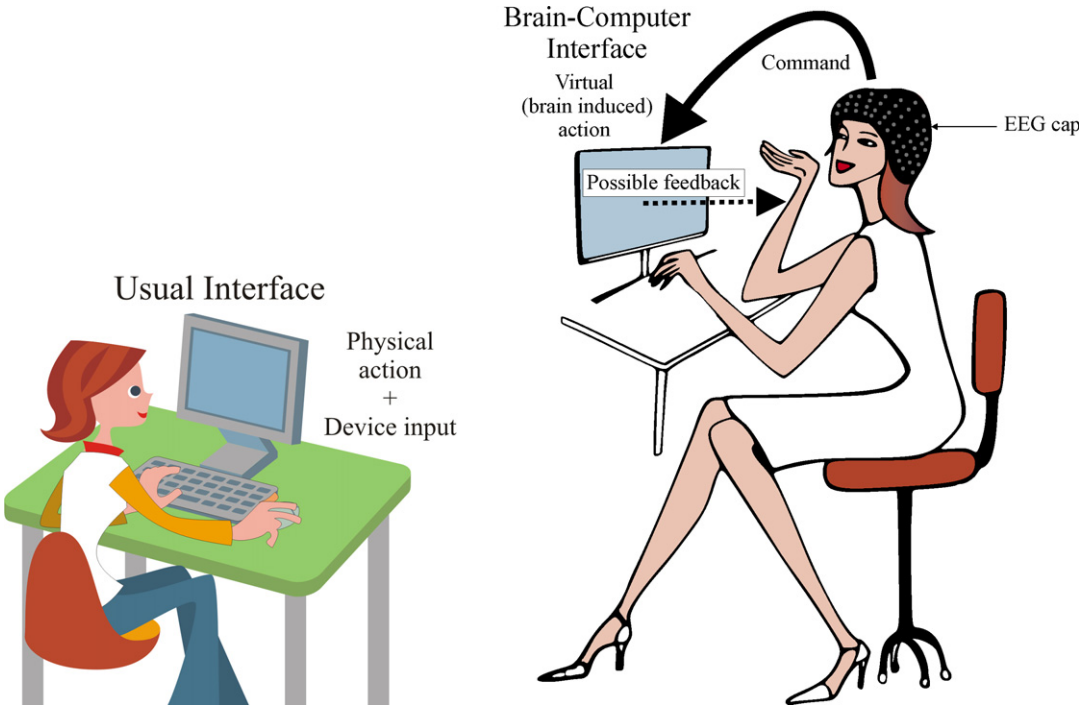

Fig. 9. Brain–computer interface as a direct communication and control channel between brain activities and its environment.

Table 2
Characteristics of recent BCI systems based on SSVEPs. ITRs are computed using Eq. (2).

Authors	Stimuli	Method	*C*	*E*	Accuracy (*M* subjects)	ITR bit/min
Gao et al. (2003)	LED	Large number of targets	48	2	87.5% (*M* = 1)	68
Kelly et al. (2005)	Flicker	Attentional effect	2	*NC*[a] (<64)	≈71%; 63–85%; (*M* = 10)	Off[a]; ≈2.3; 0.9–6.4
Lalor et al. (2005)	Chkb	AR models, Immersive game	2	2	≈89%; 71–100% (*M* = 6)	*NC*[a]; ≈15.5; 3.8–30.0
Maggi et al. (2006)	LED	Portable device	2	2	*NC*; 80–100% (*M* = 5)	≈17.2
Trejo et al. (2006)	Chkb	KPLS classifier	4	12	*NC*; 80–100% (*M* = 3)	*NC*[a]; ≈5.5; 3.8–8.0
Müller-Putz et al. (2005)	LED	Visual feedback	4	4	≈64%; 42–94% (*M* = 5)	≈5.8; 0.4–32.0
Nielsen et al. (2006)	Flicker	Auditory feedback	9	1	≈80%; 58–100% (*M* = 7)	≈21.0; 8.7–33
Wang et al. (2006)	Flicker	Time buffer, ICA lead selection, High pass threshold	13	32	*NC* (*M* = 16)	≈43; 29.0–63.1
Friman et al. (2007)	LED	Electrode combination	6	6	≈84%; 59–100% (*M* = 10)	Off[a,b]; ≈3.2; 1.3–5.2
Martinez et al. (2007)	Chkb	Visual feedback, Video game	4	6	≈96.5%; 82.3–100% (*M* = 6)	≈29.6; 17.0–38.7
Müller-Putz and Pfurtscheller (2008)	LED	Visual feedback, Commanding a hand prosthesis	4	4	≈74.7%; 55.2–90.0% (*M* = 4)	≈19.7; 4.1–34.2
Parini et al. (2009)	LED	Window length control, auditory feedback	4	8	≈97.5%; 95–100% (*M* = 11)	≈51.5; 17.0–70.0
Bin et al. (2009a)	Flicker	Lead selection	6	9	≈95%; 83–100% (*M* = 12)	≈58; 54.0–67.0
Bin et al. (2009b)	Flicker	Pseudorandom sequences	16	47	95 ± 6%	92.8 ± 14.1

Chkb, LED, and Flicker = checkerboard reversal, light-emitting diode (LED), and flickering rectangles, respectively, produced by an LCD screen. NC = not communicated by the authors; Off = offline study; *C* = number of commands accessible through the BCI system; *E* = the number of electrodes used to record the EEG; ITR = Shannon's information transfer rate.
[a] The authors selected a subset of electrodes out of 64.
[b] The purpose of this paper was to compare electrode combination methods, not to obtain a fast response.

The most common measure to assess the performance of a BCI system (and any communications system in general) is Shannon's information transfer rate (ITR). For a BCI channel with N equiprobable user commands and s commands performed per minute, where each command is correctly decoded with probability p, the information transfer rate (in bits per minutes) is given by

$$ITR = s\left[\log_2(N) + p\log_2(p) + (1-p)\log_2\left(\frac{1-p}{N-1}\right)\right]. \quad (2)$$

This equation shows that for fixed p, the ITR increases with the number of commands N. Since SSVEP-BCIs may support more user commands than other BCI systems (Wolpaw et al., 2002), SSVEPs could potentially achieve higher ITRs. Current BCI systems that are not based on SSVEPs reach a transfer rate of about 10–25 bits/min; SSVEP-based systems lead to transfer rates of 100 bits/min and beyond (Materka et al., 2007; Bin et al., 2009a,b). Moreover, SSVEP-based BCI systems can be used by more than 90% of users without much training, in contrast to most current BCI systems that do not rely on SSVEP signals (Middendorf et al., 2000; Trejo et al., 2006 or Wang et al., 2006). SSVEP-BCI systems may achieve higher information transfer rates than alternative BCI systems for the following reasons:

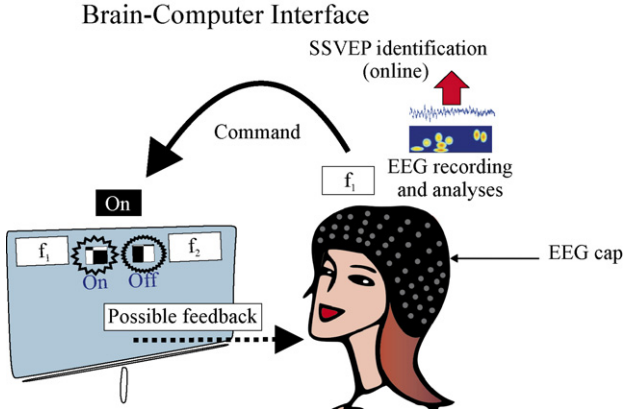

Fig. 10. Generic SSVEP-BCI system. The SSVEP signal encodes various distinct commands, and therefore, the generated SSVEP can be used to control a device.

- Increasing the number of command usually jeopardizes the classification rate, but for SSVEP-based systems this is not the case; SSVEP-BCI systems with up to 13 simultaneous commands have successfully been developed (Cheng et al., 2002; Wang et al., 2006).
- SSVEP signals are triggered by external stimuli (visual stimuli), which are more robust and easier to control than internally generated stimuli; the approach is comparable with P300-evoked potential-based BCI systems.

Recent studies on the SSVEP-BCI paradigm are listed in Table 2; SSVEP-BCI systems with 2–13 commands have been developed, with an average classification rate in the 64–96.5% range and an average ITR between 2.3 and 58 bits/min (maximal ITR 70 bits/min). As we mentioned earlier, SSVEP-BCIs tend to outperform more traditional BCI systems in terms of information transfer rates.

2.1. Taxonomy of SSVEP-BCI

2.1.1. Dependent vs. independent BCIs

The nature and extent of any BCI's dependence on muscle activity is a function of many factors, including the display, task, environment, and user (Allison et al., 2008). Most of the existing SSVEP-BCIs require eye gazing. This type of SSVEP is usually defined as a dependent BCI, because it requires neuromuscular control of head or eye movements. In contrast, the SSVEP-BCIs that are controlled by subjects' attentions are defined as independent BCIs (Allison et al., 2008; Zhang et al., 2009). This is a critical aspect of SSVEP-BCIs, because independent BCIs have a broad range of possible applications. For instance, possible end-users of BCI systems are patients with amyotrophic lateral sclerosis and patients with locked-in syndrome, who may not control their eye movements[13] and therefore might not be able to use dependent BCI systems.

2.1.2. Feature type

Most existing SSVEP-BCIs reviewed here use the spectral content of EEG signals as their main detection feature. However,

[13] Patients with amyotrophic lateral sclerosis generally have control over their eye movements, but some patients with an extremely long duration of disease (20+ years) may lose eye control, too. Patients with locked-in syndrome may not control their eye muscles; they are referred to as "total locked-in syndrome" patients.

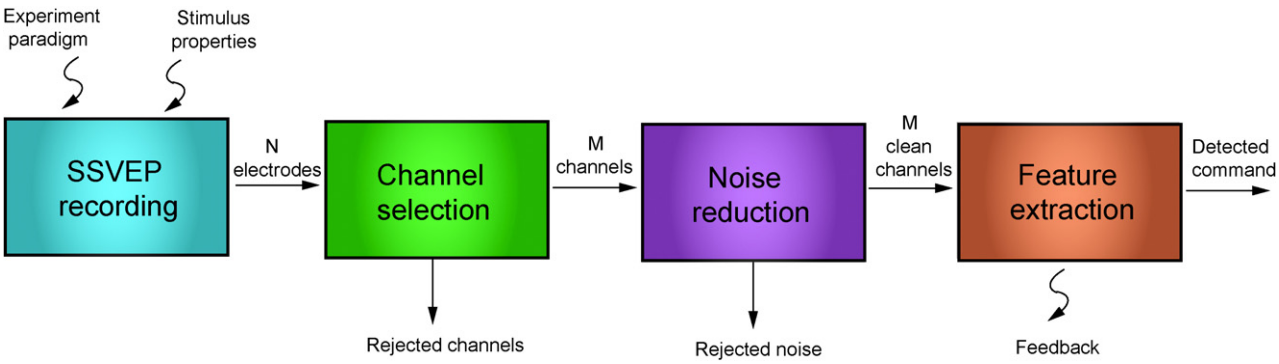

Fig. 11. Signal processing in a generic BCI system based on SSVEPs. The signal is recorded according to the experimental paradigm, with a chosen type of stimulus. Sequentially, three steps may be applied orderly: channel selection, noise reduction, and feature extraction (note that the channel selection and noise reduction steps are sometimes ignored in the literature). The output of the system is the detection of a command to execute, sometimes with feedback for the subject.

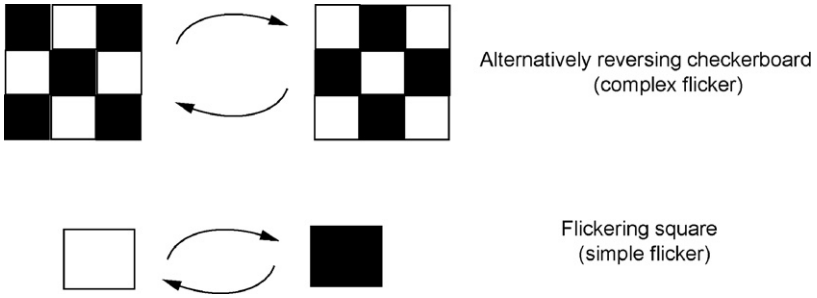

Fig. 12. Complex vs. simple stimuli.

EEG signals contain other information that might be exploited. For instance, phase information has attracted more attention in current SSVEP-BCIs (Wilson and Palaniappan, 2009). EEGs contain several dimensional aspects: time (entropy and complexity measures), frequency (spectral content, time–frequency content, local synchrony), and space (channel location, large-scale synchrony, phase, Granger causality, etc.). This leaves many options for the design of an SSVEP-BCI paradigm.

2.2. Technical aspects of SSVEP-BCIs

In the following subsections, we will provide a more detailed review on SSVEP-BCI paradigms. In order to develop a BCI system based on SSVEPs, five issues have to be addressed (Fig. 11):

1. Choice of paradigm
2. Choice of stimuli
3. Number, location, and selection of EEG channels
4. Noise reduction of EEG recordings
5. Detection of SSVEP signal

In the next subsections, we will treat these five issues.

2.2.1. BCI paradigm

The diagram in Fig. 10 depicts a generic SSVEP-BCI system. Here, we address several components of that system: choice of stimuli, number of commands, and the use of feedback as part of the training procedure.

Two types of stimuli have mainly been used so far for BCI (Fig. 12): simple stimuli (e.g., blinking light-emitting diodes or flickering squares on an LCD computer screen) and complex flickers (e.g., alternatively reversing checkerboards). Checkerboard patterns produce more pronounced SSVEPs than simple stimuli at the same frequency (Lalor et al., 2005), which is a clear advantage of complex stimuli compared to simple stimuli. However, complex stimuli have two limitations:

- Complex stimuli induce weaker high-frequency components than simple flickers do (Silberstein, 1995), and as a result, the frequency range of complex stimuli is narrower.
- Complex stimuli are larger than simple stimuli, and therefore, fewer complex stimuli can be displayed simultaneously than simple ones. Therefore, since each stimulus usually encodes one user command, complex stimuli can represent fewer user commands simultaneously than simple stimuli do. In recent BCI systems, checkerboard stimuli have been used to encode up to four commands, whereas simple flickers were used to encode up to 13 simultaneous commands (Cheng et al., 2002).

The optimal number of commands can be determined from the ITR equation; the latter implies that for detection rates below 90%, ITRs tend to decrease when more than 4 commands are used (Dornhege et al., 2004). This suggests two possible SSVEP-BCI paradigms: (a) a system with high detection rates and a small number of commands (max. 4), using complex stimuli; and (b) a system with lower detection rates but faster responses and more commands (>4), using simple stimuli. The choice depends on the purpose of the BCI system.

From an empirical point of view, it can also be observed that for a comparative number of commands, simple flickers usually obtain similar results (see ITR results in Table 2). Therefore, when more than 4 commands are needed, simple flickers seem to be preferable.

Providing feedback to subjects is a classical feature of BCI systems, which helps the subject to master the task (Cincotti et al., 2007).

It was shown in several studies that providing feedback may dramatically improve the performance of SSVEP-BCI systems (Maggi et al., 2006; Lalor et al., 2005; Piccini et al., 2005; Müller-Putz et al., 2005; Martinez et al., 2007, 2008; Parini et al., 2009) – more specifically, visual feedback (e.g., Maggi et al., 2006) or 3D game immersion feedback (Lalor et al., 2005). Contrary to other BCI systems, SSVEP-BCIs do not require feedback on brain activity of the subject. In SSVEP-BCIs, the positive effect of

feedback is purely motivational; feedback stimulates the attention or motivation of the subject (''goal-driven attention'') (Lalor et al., 2005). Because SSVEPs exploit vision processes, using other modalities for feedback is a promising approach to improve the system's stability (e.g., somatosensorial feedback in Cincotti et al., 2007).

2.2.2. Stimulus properties

Once one has selected the stimulus type according to the BCI paradigm (complex or simple flicker), one needs to find an appropriate system to generate it. Light-emitting diodes (LEDs), cathode-ray tube (CRT) monitors, and liquid crystal display (LCD) are classical stimulators used to elicit SSVEP. LED, arranged in arrays, or flashes stimulators are suitable options for single flickers, since they allow us to control the brightness of the stimuli. They may also be attractive alternatives to LCD screens, especially for high-frequency stimuli, since LCD screens usually have low refresh rates (60–70 Hz). On the other hand, LCD and CRT screens allow more freedom in terms of stimulus shape, and they are also more convenient for generating more complex stimuli, such as checkerboard stimuli. CRT refreshing rates can be high (>200 Hz), but SSVEP amplitude drops for high refresh rates.

The decided BCI complexity can be used as a criterion for stimulator selection (see Wu et al., 2008 for a detailed study):

- For low complexity BCI (less than 10 commands), LCD screens are optimal, because they induce less eye-tiredness than CRT screens.
- For medium complexity BCI (10–20 commands), LCD or CRT screens are optimal,
- For high complexity BCI (more than 20 commands), LED are to be preferred: provided that they have a short rising and descending time, they outperform LCD or CRT stimulators.

The software used to generate visual stimuli on LCD or CRT screens has to be designed carefully; the software's efficiency, accuracy, and precision should be evaluated and controlled, and these properties should also be reported in scientific papers. These properties depend on the stimulation frequencies, the number of stimulating patterns, the speed and memory capacity of the computer, and its operating system (Jaganathan et al., 2005). At last, we wish to point out that the Psychophysics toolbox (Brainard, 1997; Pelli, 1997) for Matlab®, which is a freeware toolbox available online (http://psychtoolbox.org/), can be used to generate flickering stimuli.

Once the stimulus type is chosen, in addition to the stimulus generator (LED, LCD screen, etc.), one needs to determine the optimal stimulus frequency. Since each subject is different, a reasonable approach is to choose the stimulus frequencies depending on the subject's responses. Two criteria are helpful in determining the most appropriate frequencies (Wang et al., 2005a): (a) the stability (*i.e.*, the percentage of correctly detected SSVEP signals, which is computed offline for a range of frequencies f); and (b) the signal-to-noise ratio (SNR), which is a measure that depends on the frequency f and is computed as the ratio of Fourier power at frequency f and average Fourier power at its n-adjacent frequencies (repeated from Eq. (1) for convenience):

$$SNR(f) = \frac{nF(f)}{\sum_{k=s}^{n/2} F(f + k\Delta f) + \sum_{k=s}^{n/2} F(f - k\Delta f)},$$

where f is frequency, F is the Fourier power of the signal, and Δf is the frequency step (Fourier transform precision). This definition of SNR has been shown to have similar numerical values (Wang et al., 2006) for the three frequency subsystems (low, medium, and high frequencies). Moreover, frequencies close to the alpha range have poor SNRs near the spontaneous EEG alpha peak[14]. Offline detection was above 95% in medium (31–35 Hz) or high-frequency (39–45 Hz) regions; however, one should take into account that muscular activity becomes more pronounced at higher frequencies.

Finally, one may combine several frequencies in the stimulus to induce quadratic phase coupling, resulting in unique and complicated responses, even though only a few distinct frequencies may be involved (Srihari Mukesh et al., 2006). Such an approach may also improve the stability of the BCI system.

2.2.3. Channel selection

SSVEPs can, in principle, be recorded over the whole scalp. However, SSVEPs are typically the strongest in the visual cortex (especially V1 area), and therefore, occipital electrodes usually have the highest signal-to-noise ratio. When designing a BCI system, one needs to choose the number and location of electrodes (Müller-Putz et al., 2008). Obviously, the fewer electrodes, the more user-friendly the system will be, giving a practical advantage to the channel selection method over a modeling approach. Once the number and location of the electrodes have been selected, one needs to design a method that is able to extract SSVEPs from EEG signals recorded from those electrodes.

Several methods of this kind have been suggested:

- Best classification results are usually reached by using a bipolar derivation (Wang et al., 2005b; Lin et al., 2006; Friman et al., 2007; Müller-Putz et al., 2008). Some methods select an ''optimal'' subset of electrodes. In the method of (Wang et al., 2005b), one bipolar pair of electrodes is selected to maximize SSVEP power. An alternative method uses canonical correlation analysis (CCA) to extract multiple bipolar electrode pairs that maximize SSVEP power (Lin et al., 2006). The latter method was shown to outperform the former, probably because it uses more electrodes. Recently, Friman et al. (2007) proposed a method, referred to as minimum energy combination, which goes beyond pairs of electrodes and considers larger collections of electrodes. Finally, instead of considering the spatial and spectral information independently, one can design spatial filters to integrate multiple electrode information (Garcia-Molina et al., 2009).
- Other methods try to extract independent sources. First, independent sources are extracted online through independent component analysis (ICA). Next, one or more sources maximizing the SSVEP (in relative power) are retained for SSVEP detection (Li et al., 2003; Wang et al., 2004, 2006), while the other sources are discarded as noise.

These different methods have not been compared so far. ICA is the best-known and most-documented method. Moreover, it has the great advantage of simultaneously performing electrode selection and noise reduction (see Section 2.2.4). In the absence of a comparison of the different methods, the most-documented method (ICA) remains *a priori* the most recommendable. However, doubts have been raised about ICA, especially in the context of BCI systems; statistical independence may not be a valid assumption, and it is not always obvious how to rank the independent sources (Friman et al., 2007).

2.2.4. Noise reduction

EEG signals are noisy and contain artifacts; muscular activities; movement artifacts; electrical pulse noise; and electrodermal, electrovascular, and respiratory signals may interfere with brain signals. In addition to these extracerebral signals, brain activity that

[14] The SSVEP amplitude is typically high in the alpha range, but spontaneous EEGs also have large amplitudes in that range. Many studies use 10 Hz SSVEPs, motivated by their high amplitude; however, the SNR is not necessarily high at that frequency, due to spontaneous EEGs.

is not related to SSVEPs is also considered as noise; indeed, we encode information in SSVEPs, and all other signals are therefore treated as noise. Muscular activities may be detected with electromyographic sensors or by analyzing high-frequency band EEG signals (90–150 Hz activity, Pivik et al., 1993). Subjects may be trained to relax and control their movements through feedback, and corrupted signals may be rejected. Recently, alternate half-field stimulation was introduced as an alternative noise rejection method. Two stimuli are flashed alternatively at the same frequency in each visual hemifield, and the signals recorded by O1 and O2 are subtracted. The VEPs in O1 and O2 should have different phases, but the phases of EMGs and spontaneous EEGs in those two signals should be similar. Therefore, subtracting O1 and O2 mostly eliminates EMGs and spontaneous EEGs. This method was successfully used to enhance the SNR of a 4-command BCI (Materka and Byczuk, 2006).

In order to enhance SSVEPs, several signal processing methods have been suggested. A first approach is to apply adaptive filters. The SSVEP is a sinusoidal signal (or more generally, a periodic signal) buried in an EEG, and the objective is to extract that signal. A common approach to that problem is to tune a filter to the sinusoidal component, which was shown to improve the SSVEP extraction dramatically (7–10 dB improvement, Davila et al., 1994). This approached is called adaptive line enhancement (ALE). Several alternative approaches are based on the fact that an EEG is recorded by several electrodes distributed over the scalp: Laplacian filtering in combination with notch filtering (Tang and Norcia, 1994), adaptive eigenfilter (Davila and Azmoodeh, 1994), multivariate magnitude-squared coherence (Ghaleb et al., 1996), and, more recently, ICA (Li et al., 2003; Wang et al., 2004, 2006). As mentioned above, in the absence of a comparative study, the most-documented method is probably the most reliable. ALE and ICA seem to be the most-documented methods, and therefore, we consider them as the most commendable candidates at the moment.

2.2.5. Detection

SSVEP studies in neuroscience typically only use classical methods to identify the evoked response: superposition, averaging, frequency analysis, or correlation analysis (Spekreijse et al., 1977). For BCI applications of SSVEPs, frequency analysis is usually the most appropriate. Frequency analysis of SSVEPs is significantly different from standard EEG frequency analysis, because the experimenter usually has substantial a priori knowledge about the SSVEP signal at hand (see Bach and Meigen, 1999 for a review about frequency analysis of SSVEPs). Narrow band Fourier power or narrow band filtering (such as ALE, described in Section 2.2.4) is often applied to extract frequency information. Detection is usually done by thresholding—SSVEPs are detected if the power at the SSVEP frequency, integrated over a time window of length L, is above a certain threshold; the latter is computed from the spontaneous EEG spectral distribution (Cheng et al., 2005), following the general principle of z-score processing (see *e.g.*, Browne and Cutmore, 2002). The choice of integration period L of the Fourier transform is a tradeoff between noise reduction and bias (Silberstein, 1995). To add flexibility to the system, one may reset a time buffer every time a command is detected (*e.g.*, in Wang et al., 2006), when the time buffer is 8 s long. As a result, the reaction speed of the BCI system automatically adapts to the user.

3. Open questions and challenges

3.1. General open questions

During stimulation with long trains of flickering light, the system can attain a dynamic steady-state throughout the duration of the recording period without ever returning to its resting state: the steady-state visually evoked potential (SSVEP). Due to their properties, SSVEPs can be easily quantified and reproduced. They find numerous applications in neuroscience. In the last 40 years, many studies were devoted to, or based on, SSVEP paradigms. Nevertheless, the basic properties are not yet fully understood. Some crucial properties of SSVEPs need further investigation—namely, frequency range, long-term effects, and SSVEP paradigms. The key word to remember is consistency—from one study to another, several properties of the paradigm are changed; consequently, meta-analyses become arduous.

Let us start with some open questions related to the frequency range in which SSVEPs occur. Most investigations concerning the generation of SSVEPs are restricted to one of the three SSVEP components (centered at about 10, 20, and 40 Hz). It has been emphasized that the dipolar activity over the posterior scalp depends on the stimulation frequency (Müller, 1998). The dipole localization of each SSVEP component is poorly documented. Furthermore, the effect of combined frequencies within a stimulus on source location has not yet been investigated. If we want to understand the properties of SSVEPs, investigations and comparisons of several frequency ranges should become the norm instead of remaining the exception.

The frequency range of SSVEPs is by consensus considered to be 3–40 Hz. Recent studies, however, have reported SSVEPs in scalp EEGs from 1 to 100 Hz. This corresponds to a general tendency in EEG studies in which new systems and signal processing techniques have allowed the study of very high-frequency ranges. The existence of SSVEPs in low-frequency ranges is only rediscovered and seems well established (e.g., Regan and Regan, 1988). High-frequency responses are very novel and raise questions about the recording limits of scalp EEGs. Frequency ranges higher than the traditional gamma range (25–40 Hz) have recently been investigated; for instance, using intracranial EEG, it was observed that 60–200 Hz rhythms may be related to attention (Brovelli et al., 2005). A similar frequency range was investigated with human subjects using MEG (Gunji et al., 2007); it was shown that storage and rehearsal processes of singing correlate with a decrease of oscillatory activity at high frequencies. Consequently, where should we place the limit of scalp EEG recordings? It is still unclear whether SSVEPs can be generated at high frequencies in the gamma range or higher. Obviously, studies, such as Herrmann (2001), Birca et al. (2008) and Asano et al. (2009), should be replicated in order to confirm the existence and investigate the properties of probable high-frequency responses (latency, amplitude and phase topography, reaction to color stimuli, source location, etc.).

At last, SSVEPs may allow us to address many open questions related to alpha rhythms (see Section 1.7.4). This direction of research is crucial for EEGs, as the alpha range (discovered by Hans Berger in 1924) is the oldest documented and maybe the most notorious brain rhythm; nevertheless, the alpha rhythm remains poorly understood. Surprisingly, alpha harmonics are correlated with all modalities of SEPs (c.f. Sections 1.7.4 and 1.9), with peaks at 10, 20, 40, and probably 80 Hz for SSVEPs; peaks at 40 and 80 Hz for ASSRs; and a peak at 20 Hz for SSEPs. This seems to indicate a general brain phenomenon related to alpha range activity, whose mechanisms are not yet well understood, which could establish relationships between frequency ranges (alpha-beta or alpha-gamma interactions).

Similar investigations could be conducted in other frequency ranges—for instance, in the 40 Hz range, which has been conjectured to be involved in the binding process (see Başar et al., 2000 for review); one may, for example, investigate whether SSVEPs at 40 Hz disturb or enhance visual binding. Along the same lines, LCD screens have been reported to induce SSVEPs in intracranial EEGs at their refresh rate (usually 60–70 Hz; Krolak-Salmon et al., 2003). Little is known about the long-term effect of this passive LCD-elicited SSVEP on the human brain, especially in

regard to brain disorders (c.f. especially Section 1.8.8). It is well known in psychophysiology that a repetitive stimulus tends to induce a long-term adaptation of neuronal systems. SSVEPs are not an exception to this rule, and flicker adaptation can be observed (Bergholz et al., 2008). Nevertheless, long-term adaptation to environmental flickering lights (such as neon lights) and their possible effects are not documented.

We now comment on open questions related to the different SSVEP paradigms:

- Each stimulus type (LED, checkerboard, gratings, etc.) induces a specific response. There is a wide diversity of stimuli used and an absence of consistency between the reviewed investigations (c.f. Section 1.5). However, a systematic study comparing source localization for each of these stimulus types is missing (especially simple *vs.* complex stimuli).
- Finally, the stimulation duration may have a strong effect on the recorder SSVEP. When studies on periods as disparate as 500 ms (Pastor et al., 2003) or 50 s (Srinivasan et al., 2006) are led, it is natural to wonder how SSVEP activity evolves along time. Broadly speaking, investigations concerning the time evolution and the dynamics of SSVEP sources and topography are not sufficiently advanced (Nishifuji et al., 2006). For instance, whereas efficient tools for time–frequency analysis were used proficiently for many evoked response investigations (e.g., see Tallon-Baudry et al., 1996), very few time–frequency analyses of SSVEPs have been led (for instance, Cui and Wong, 2006a,b). Similarly, information flows provide appreciable leads about SSVEP dynamics (for instance, using directed transfer functions; Wehling et al., 2007).

3.2. BCI challenges

In the application of SSVEPs to BCIs, the EEG signals are recorded at occipital brain areas while subjects focus on flickering light stimuli at different frequencies, each encoding a different command. By detecting the frequencies in the recorded EEG signals, one can retrieve commands to pilot a computer or a machine. BCI systems based on SSVEPs may be studied from two different viewpoints: applied research (engineering) and basic research (neuroscience). BCIs have, so far, mostly been investigated from the point of view of applied research.[15] Finalized applications (industrial-level quality) should logically be the next challenge for SSVEP-BCI applications. The two key issues in this context are stability and performance (c.f. Section 2); a BCI system is stable if it makes few errors (low error rate), and its performance is good if it provides fast commands (high ITR).

- The first issue (stability) may be solved by signal processing, but maybe new paradigms can also enhance the SNR of SSVEPs (see above, visual hemifield stimulation in Section 2.2.1 or coupled multiple frequency stimulation in Section 2.2.2).
- The second issue (performance) depends mostly on the experimental design.

In other words, experimental design and paradigms are crucial if one seeks to develop efficient SSVEP-BCI systems. Unless a better understanding of the underlying mechanisms of SSVEPs is obtained, experimental design will not be significantly improved. Consequently, basic research studies of BCIs are increasingly needed in order to provide reproducible and controlled results. For example, a thorough investigation of the effects of each experimental parameter is needed: size of the stimulus, distance to the stimulus, brightness, mental fatigue, etc. Without such study, uncontrolled parameters may distort results. Studies of this kind are challenging due to their interdisciplinary nature, involving both biological and engineering aspects. Similarly, as already stated above (Section 3.1), the long-term effects of SSVEPs are not documented. If SSVEP-BCI systems are to become available to the public at large, it is crucial to assess such adaptation effects beforehand.

Finally, practical applications of SSVEP-BCI require the optimization of two additional parameters: the system cost and ergonomics (the BCI system must both be cost-effective and user-friendly). Recent investigations already discus these parameters (Piccini et al., 2005; Jia et al., 2007; Wang et al., 2008), which demonstrates how close we are from industrial practical applications.

3.3. Conclusion

The SSVEP is an exciting research paradigm, with numerous applications. Although brain activity is well documented, several questions remain open. Basic science about SSVEPs needs to be modernized and studied with more details. Moreover, modern machine learning and signal processing tools offer new techniques to extract and study SSVEP. This experimental paradigm offers opportunities for novel and important investigations.

[15] The balance of scientific literature about BCI-SSVEPs is more than 4-to-1 in favor of applications.

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