



Neuroelectric Correlates of Human Sexuality: A Review and Meta-Analysis

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Abstract

Many reviews on sexual arousal in humans focus on different brain imaging methods and behavioral observations. Although neurotransmission in the brain is mainly performed through electrochemical signals, there are no systematic reviews of the electrophysiological correlates of sexual arousal. We performed a systematic search on this subject and reviewed 255 studies including various electrophysiological methods. Our results show how neuroelectric signals have been used to investigate genital somatotopy as well as basic genital physiology during sexual arousal and how cortical electric signals have been recorded during orgasm. Moreover, experiments on the interactions of cognition and sexual arousal in healthy subjects and in individuals with abnormal sexual preferences were analyzed as well as case studies on sexual disturbances associated with diseases of the nervous system. In addition, 25 studies focusing on brain potentials during the interaction of cognition and sexual arousal were eligible for meta-analysis. The results showed significant effect sizes for specific brain potentials during sexual stimulation (P3: Cohen's $d = 1.82$, $N = 300$, LPP: Cohen's $d = 2.30$, $N = 510$) with high heterogeneity between the combined studies. Taken together, our review shows how neuroelectric methods can consistently differentiate sexual arousal from other emotional states.

Keywords Sexual arousal · Electrophysiology · Sexuality · Neuroelectricity · Sexual preference

Introduction

Sexual topics have always enjoyed a special place in human culture and managed to capture all aspects of human curiosity (Conard, 2009). Famous artists, the entertainment industry, and of course scientists have shown interest in the subject, and empirical work has covered a variety of aspects ranging from sexual harassment in insects (e.g., Teseo, Veerus,

Moreno, & Mery, 2016) to comparisons of sexual activity between different nations (e.g., Prendergast et al., 2016). With the human brain as the most complex organ known to man and the modern rise in neuroscientific research interest (Huang & Luo, 2015), the role of the human brain in human sexual behavior has also become the subject of many scientific experiments (Baird, Wilson, Bladin, Saling, & Reutens, 2007; Georgiadis & Kringelbach, 2012). Nevertheless, the uniqueness and complexity of human sexuality are still not fully understood, with debates about its basic aspects still going on to date (Bailey et al., 2016; Savin-Williams, 2016).

To investigate sexuality in the human brain, neuroscientific methods like functional magnetic resonance imaging (fMRI), positron emission imaging, magnetoencephalography (MEG), single-photon emission computed tomography (SPECT), and electroencephalography (EEG) have been used extensively. While imaging methods allow for a spatially precise visualization and localization of cortical areas involved in sexual behavior, electrophysiological methods capture neuroelectric processes with a higher temporal resolution allowing for hypotheses about the neuronal activity and its exact temporal scale at millisecond level. Sexual processes

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influence human cognition subliminally (Legrand, Del Zotto, Tyrand, & Pegna, 2013), in a matter of milliseconds and in the earliest processing stages (Ortigue & Bianchi-Demicheli, 2008), yet no work has summarized electrophysiological results capturing the entire diversity of neuroelectric investigations into human sexuality so far. There are only a small number of reviews that highlight specific topical aspects within sexuality and in which electrophysiological measurements were mentioned (e.g., Bianchi-Demicheli & Ortigue, 2007; Gola, Wordecha, Marchewka, & Sescousse, 2016; Ortigue, Patel, & Bianchi-Demicheli, 2009).

The present work provides a systematic review of the international literature on neuroelectric measurements or stimulations related to any form of human sexual behavior. The emphasis is not on evaluating support for different concepts and theories developed in the literature but rather to summarize all reports on neuroelectricity related to any form of human sexuality. Animal studies were excluded with a focus on human studies only. Other peripheral electrophysiological measures with human samples, such as electrocardiography, electromyography, or measurements of the skin conductance response, have also been commonly used in order to investigate human sexual behavior (e.g., Rosen, Goldstein, Scoles, & Lazarus, 1986; Sarrel, Foddy, & McKinnon, 1977). These methods (i.e., electrocardiography, electromyography, or skin conductance response), however, would deserve their own reviews and will not be discussed within the present summary. Rather, the present literature search was restricted to studies on cortical electric stimulation and recording since these measures are assumed to be more reliable indicators of human sexual behavior and less prone to potential influences on behalf of the individual than peripheral electrophysiological properties (Simons, Öhman, & Lang, 1979). The goal of the present summary was to provide a first extensive overview on the matter and to identify possible limitations within the field while highlighting methodological and theoretical directions for future research.

Method

After an initial overview to identify technical terms as key words to outline the topic semantically, a systematic search was conducted in September 2017 using the formula: (EEG OR ERP OR event-related potentials OR somatosensory OR brain potentials OR DBS OR deep brain stimulation OR neurofeedback OR tDCS OR transcranial direct current stimulation OR electroconvulsive) AND (sexual OR sexuality OR attractive OR erotic OR orgasm OR pleasure OR sleepsex OR sexomnia OR impotence OR genital OR sexual dysfunction OR ejaculation OR paraphilic OR pedophilia OR pedophilic OR exhibitionism) OR [(epilepsy OR seizure) AND (sexual OR orgasm OR fetish OR transsexual OR exhibitionism)].

This formula was used in PubMed, PsycINFO, PSYINDEX, PsycARTICLES, Google Scholar, Scopus, Web of Science, and works in English, German, French, Italian, Portuguese, Russian, and Chinese were included in the results. The search went on through all lists of references from the initial findings until no new work was found. Recommendations by colleagues were also included. Apart from peer-reviewed articles and case studies, findings include results published in book chapters, dissertations (sometimes only partially published later), or abstracts. Since attempts were made to only reference latest editions, there can be considerable gaps in time between the year in which the latest edition was published and the year the experiment was actually conducted. The experiment reported in Langevin (2014), for instance, is the same one already reported in the earlier edition (Langevin, 1985). The search resulted in 255 reported studies covering 81 years of research (1936–2017). The findings stem from heterogeneous thematic fields capturing the high diversity of contexts in which electrical signals related to sexuality played a role in research. The identified studies focused on electric stimulations of cortical areas associated with genitalia or sexual functions (28), peripheral electric stimulation of genitalia with simultaneous electrocortical recordings (10), or electrocortical recordings during erections or orgasm (12). Other studies focused on cognitive tasks in mostly healthy participants involving visual, auditory, or olfactory sexual stimulation (127). Similar experiments were also conducted with subjects displaying abnormal sexual preferences (16). Another group of neurological studies focused on epileptic patients with seizures involving sexual behavior (65) or at electrocortical recordings of sexual behavior during sleep in sleep disorders (6). Further studies, some of them highly controversial, describe attempts at manipulating sexual orientation or preference (11). Many studies combine more than one of the topics aforementioned. Table 1 gives an overview over the most common methodological terms and concepts as well as their significance within this review. We excluded studies on transgender and transsexualism and expressions of the opposite gender (e.g., cross-dressing) unless this topic was researched in epileptic samples. All pertinent results will be listed in the thematic order given above, but with some exclusions aside from studies that may have been missed.

Some neuroelectric studies on gender differences (e.g., Hanlon, Thatcher, & Cline, 1999) may also capture differences in sexual preferences but mostly focus on describing gender differences in cognitive task-performance using EEG (e.g., Razumnikova, 2004) and were thus not considered in this review. Studies investigating different sex roles (Berfield, Ray, & Newcome, 1986) or focusing on gender identification tasks (e.g., Sun, Gao, & Han, 2010) were also excluded. A further issue was the sexual stimulation itself. When an experimental manipulation comprised a broad positive stimulation of the participants through, for example, pleasant

Table 1 Technical terms and definitions

Term	Abbreviation	Definition and significance
<i>Recording methods</i>		
Electroencephalography	EEG	A very common noninvasive method in neuroscientific research which measures electric activity of the brain. Electrodes are typically placed on the scalp and record voltage fluctuations. These fluctuations are assumed to result from postsynaptic potentials of pyramidal cells. Such potentials create a shift of electrical charges along the cells and act as a small dipole. Thousands of similarly oriented dipoles like this create a measurable amount of voltage on the scalp (Luck, 2014). Sometimes electrodes are also placed within the brain allowing for intracranial recordings of voltage fluctuations within specific brain regions. An advantage of EEG is its high time resolution. EEG has been used extensively to research human sexuality
Event-related potentials	ERP	The most commonly used EEG measure to research the effect of sexual stimuli on the brain and cognition. Usually sexual stimuli (visual, auditory, olfactory) are displayed and perceived without direct physical contact, while continuous EEG is recorded in an experimental setting. EEG segments where response to a sexual stimulus was recorded are then averaged and compared to the averaged signals of other stimuli. Averaging, for example, 60 such responses toward a sexual stimulus makes it possible to relate this averaged signal to the event of a sexual stimulation. These averages are the so-called ERP of sexual stimulation derived from the ongoing EEG activity (Luck, 2014). Many prominent ERP components have been discovered in ERP research and used to research sexuality with high temporal resolution
Contingent negative variation	CNV	The CNV is an ERP component assumed to represent cognitive anticipation and expectation toward a stimulus (Walter et al., 1964). In a typical experimental setting, continuous EEG is recorded and the subject knows that at a certain point a sexual stimulus will be presented. The ERP segments right before the onset of this sexual stimulus are used for averaging, and the resulting CNV can be used to compare anticipation toward sexual stimuli with anticipations of other types of stimuli
Feedback-related negativity	FRN	The FRN is an ERP component assumed to represent an evaluative process following a presentation of a feedback (Miltner et al., 1997). In an experimental setting usually choice or decision tasks are used, and the subjects receive a feedback for their decision. The FRN is usually averaged during this feedback stage. Using such experimental designs, the FRN in response to a feedback given by an attractive person can be compared to the FRN when an unattractive person is giving the feedback. Such experiments mostly use visual depictions of attractive and unattractive human faces combined with the feedback. Sexual pictures of whole bodies have not been used
Mismatch negativity	MMN	The MMN is an ERP component assumed to represent violations to sensory regularities (Näätänen et al., 1978). In an experimental setting, a series of, for example, sexual stimuli are used to create a sense of regularity and subjects familiarize themselves with this pattern and create expectations. Then a deviation from this familiarized pattern is typically introduced and the resulting ERP to this deviation is averaged to form the MMN. The MMN to deviations from sexual stimuli can be compared to MMN to deviations from other types of stimuli. Although a promising ERP component, the MMN has rarely been used to study sexuality
Somatosensory evoked potentials	SEP	A special form of ERP where the stimulation consists of actual physical contact. Instead of showing pictures or producing sounds, stimulation is done by either touch or electric stimulation. The so-called SEP are measured and averaged in similar ways as the ERP. Using this method, somatosensory stimulation of the genitals with stimulating electrodes (e.g., Bradley et al., 1998) can be compared to stimulations of other nerves on the body

Table 1 (continued)

Term	Abbreviation	Definition and significance
Quantitative electroencephalography	qEEG	Instead of averaging EEG segments that are timely related to an external event, there are also ways to calculate induced oscillations that are not phase-locked or evoked, but the result of either more complex stimulation, for example, film sequences or the result of a stationary resting state recording without stimulation (Cohen, 2014). Such activity is better represented in the frequency domain, and Fourier transformation is a very commonly used method to transform EEG signal from the time domain to the frequency domain. This transformation allows for the analysis of different neural oscillations. Temporal information is often sacrificed or not considered. A variety of such EEG frequencies (e.g., delta: < 4 Hz, alpha: 7.5–12.5 Hz, gamma: 30–40 Hz) have been related to cognitive functions (Klimesch, 1999) or psychopathology (Newson & Thiagarajan, 2018). Earliest EEG experiments have shown a decrease in occipital alpha activity when subjects were exposed to light (Berger, 1929; Jasper, 1936), and alpha activity was later constantly related to cortical inactivity. Different alpha activities between the two brain hemispheres were frequently investigated with erotic films or during masturbations to draw conclusions about hemispheric asymmetries in terms of brain activity and sexuality. Synchronization in the theta band (4–7.5 Hz) was assumed to reflect good cognitive performance, and in rare cases this frequency was used to compare the processing of sexual stimuli to the processing of other non-sexual stimuli (e.g., Doppelmayr et al., 2003). High-frequency activity (e.g., beta: 22–30 Hz) is often enhanced during cognitive processes, and some studies have focused on erotic films and their influence in the down-regulation of such frequencies (Lee et al., 2010)
Source reconstruction	–	The recorded scalp potentials can also be used to reconstruct dipoles with magnitudes, orientations, and specifically locations within the brain. A variety of methods have been developed to reconstruct the sources of scalp potentials within the brain (Grech et al., 2008). Using such methods, an ERP related to sexuality or specific EEG frequencies during a sexual film can be related to specific brain regions. Such localizations also allow to associate findings from EEG studies on sexuality with other findings gained from methods with high spatial resolution (e.g., fMRI)
Magnetoencephalography	MEG	A less commonly used noninvasive method to measure signals of the brain is the MEG. The electrical activity generated by intra- and extracellular currents of the pyramidal cells also generates a magnetic field (Hämäläinen et al., 1993). This magnetic field can be recorded with MEG and with a higher spatial resolution. Using sexual pictures in an experimental setting, visual-evoked magnetic fields can be calculated similarly to the ERP in EEG. Such averaged signals can then be compared to signals from other non-sexual stimuli
<i>Stimulation methods</i>		
Deep brain stimulation	DBS	DBS uses implanted electrode leads in the brain to deliver an electric current and the amount of current determines the size of the brain tissue stimulated (Miocinovic et al., 2013). The output from a stimulated nucleus is increased which results in a complex cascade of excitatory and inhibitory effects. Early experiments tried to map cortical functions and also encountered somatosensory regions related to the genitalia. Later developed stereotaxic devices for humans allowed for stimulations of deeper subcortical regions in the brain (Spiegel et al., 1947). In some surgical studies using DBS side effects related to sexuality have been reported
Electroconvulsive therapy	ECT	Originally used in 1939 as a treatment method in psychiatry, ECT was called electroshock therapy and its use has been extensively debated (Cerletti, 1950). In principal, ECT creates an electrical current that traverses brain tissue and evokes a grand mal seizure. The exact mechanism, physiological consequences, and therapeutic effects are still debated (Bolwig, 2011). In rare cases, this method has been used to treat sexual dysfunction
Transcranial direct current stimulation	tDCS	Using a pair of surface electrodes, motor-evoked potentials can be produced through electrical pulses (Merton & Morton, 1980). Modern tDCS methods noninvasively apply weak direct currents over the skull from which approximately 50% enters the brain (Dymond et al., 1975). This can induce focal, reversible changes in cortical excitability with only minor side effects presumably caused by current not passing through and only flowing between the scalp and the electrode (e.g., dizziness, itching; Nitsche et al., 2008). The duration of tDCS effects depends on the applied current density but is typically not more than 20 min. This method has rarely been used in experiments with sexual images

Table 1 (continued)

Term	Abbreviation	Definition and significance
Transcranial magnetic stimulation	TMS	Strong and brief external magnetic fields were shown to stimulate the human motor cortex without the side effects of distress or pain (Barker et al., 1987). Modern TMS methods use a coil of wire through which an electric current passes, generating a magnetic field (Nollet et al., 2003). This field can then modulate currents within an electrically conductive tissue such as the brain. Modulation is assumed to occur through depolarization of fast-conducting fibers such as the pyramidal tracts (Nollet et al., 2003). Safety issues (occasional seizures) have only rarely been reported (Belmaker et al., 2003). This method has not been used often to influence sexual reactions or treat sexual dysfunction

pictures of babies in combination with erotic scenes, without the possibility of separating the two categories in the experiment, we excluded the study. Although such studies are sometimes cited as support of specific effects of erotic imagery on cognition, they actually used a mixture of erotic and non-erotic stimuli to invoke a pleasant experience, contrary to recommendations (Ortigue & Bianchi-Demicheli, 2008). Consequently, such studies do not make clear inferences about a distinct erotic stimulation (e.g., Ferrari, Bradley, Codispoti, & Lang, 2011; Ferrari, Codispoti, Cardinale, & Bradley, 2008; Flaisch, Junghöfer, Bradley, Schupp, & Lang, 2008; Keil et al., 2001; Simons, Detenber, Cuthbert, Schwartz, & Reiss, 2003). Conversely, studies labeling a picture category as “pleasant” while it contained only images of erotic couples and opposite-sex nudes were included (e.g., Tamm, Uusberg, Allik, & Kreegipuu, 2014). We did not exclude studies that used images of attractive faces without bodies as a positive visual stimulation since those stimuli have also a sexual relevance. One study involving EEG measurements in relation to erotic content was excluded since it included only an abstract of a research proposal without actual collected data or results (Ortiz & Mariiez, 2013). For similar reasons, another proposal (Prause, 2013) and a work on EEG and orgasmic conditioning (Khan et al., 2011) were excluded. The latter only summarizes statements on the amount of research on the topic in form of an abstract. A work by Cartwright, Bernick, Borowitz, and Kling (1969) examined the effects of erotic movies on sleep, while EEG was being recorded, but the study only mentions EEG in the methods part without reporting any EEG results. The same applies to Prause, Staley, and Fong (2013). Consequently, the studies by Cartwright et al. (1969) and by Prause et al. (2013) were excluded. Two other study abstracts (Radilová, Figar, & Radil, 1983, 1984) provide reports on the effects of sexual imagery on EEG but both report on the same experiment so only the first one is mentioned throughout this review. Furthermore, preliminary results in book chapters or abstracts from later published finished work or results in dissertations with later publications were excluded (e.g., Lang, 1978 reporting preliminary results from Simons et al., 1979, and Tucker, 1983 reporting them from Tucker & Dawson, 1984)

unless they provided further results or statistics not shown in the later publication (e.g., effect sizes). Cohen, Rosen, and Goldstein (1985) refer to Hirshkowitz, Ware, Turner, and Karakan (1979) as a study reporting results on cerebral asymmetry during erections but after inspection of Hirshkowitz et al. no conclusive mention about erectile function and EEG was found. Therefore, the study by Hirshkowitz et al. did not meet the criteria to be discussed here. Lastly, a report on EEG laterality of compulsive sexual misconduct (Rosen, Fracher, & Perold, 1979) could not be traced since it probably consists of an unpublished conference report.

Where possible, data were aggregated through meta-analysis. Given the heterogeneity of samples and material, the notion of a single true population parameter (as in a fixed-effect model) seemed implausible. Therefore, a random-effects model was chosen. Studies were weighted using the DerSimonian–Laird method (i.e., each study is weighted by its inverse total variance, that is, by the inverse sum of its own variance and the between-study variance). The effect sizes to be pooled were derived from the η^2 coefficient of one-way repeated-measures analyses of variance (ANOVAs). (Note that partial η^2 equals η^2 for one-way ANOVAs, as Lakens [2013] points out.) The accuracy of the (partial) η^2 coefficients reported was checked given the F ratio and its numerator and denominator degrees of freedom (df), that is, the df_{effect} and the df_{error} , respectively. The conversion from F , df_{effect} , and df_{error} to η^2 was made using formula 13 from Lakens (2013; cf. Cohen, 1965). This led to slight corrections of the (partial) η^2 for two studies (Mastria, 2014 [Exp. 2]; Uusberg et al., 2014). The (partial) η^2 coefficients, in turn, were converted into f values through $f = \sqrt{\eta^2 / [1 - \eta^2]}$ (Cohen, 1988, p. 281). Finally, the f values were converted into standardized mean differences (d) using the formulae by Cohen (1988, pp. 277–280) for the case of maximum variability. The standard error (SE) of d was estimated using the formula provided by Lipsey and Wilson (2001).

The meta-analysis was conducted using the *metan* command within STATA, version 11.2 (StataCorp, College Station, TX, USA). Furthermore, potential publication bias was checked graphically using the *metafunnel* command within

STATA. Finally, Egger's test, a statistical test of funnel plot asymmetry (null hypothesis: no preponderance of effects from small studies), was carried out using the STATA command *metabias* (Harbord, Harris, & Sterne, 2009). According to Harbord et al., such tests of funnel plot asymmetry should not be used if the number of studies included in the meta-analysis was less than 10.

Results

Neuroelectricity and Genital Physiology

Electric signals through neuronal pathways play a vital role in the control of genital functions in humans. Table 2 lists all the studies conducting electrical stimulation of the human cortex resulting in sensation near the genital area or some form of erotic sensation. The reverse route was examined by a number of studies using electrical stimulation at the genitalia while recording electrical signals on the scalp or intracranially (see Table 3). Additionally, some studies looked at the neuroelectric processes during physical genital self-stimulation and orgasm (see Table 4). The studies range from a collection of earliest invasive examinations of the human cortex to modern event-related potential (ERP) studies.

Electrophysiological Localization of Genitals in the Human Brain

After the first morbid experimental electrical stimulations (Fritsch & Hitzig, 1870) showed predictable movement in a living dog, the concept of the motor cortex has also been investigated in man. The assumption was that primary motor centers would be similarly located in man. Earliest reported human electrophysiological studies with sexual relevance aimed at basic localization of brain tissue with sensorimotor function. Other investigations aimed at measuring conduction velocities of nerves. Naturally in such studies, cortical representations of the genitals were occasionally encountered and reported (Foerster, 1936; Penfield & Jasper, 1954; Penfield & Rasmussen, 1950; Scarff, 1940). The preferred method comprised invasive cortical stimulations on open brains with self-reports on induced peripheral sensation as well as other peripheral measures in awake epileptic patients. The postcentral areas of the brain with somatosensory properties were the main target area in such experiments. The product of such early work on motor and sensory cortices is now well known as the homunculus diagram, serving as a somatosensory map to this day, even if the concept of somatotopy displayed by such diagrams renders a vast oversimplification of cortical limb representations (Schieber, 2001) and has been criticized (Schott, 1993). Interestingly, the genitals themselves are initial and obvious hints to a probable fallacy of the somatotopic

continuity initially proposed (Feinsod, 2005; Kell, 2005; however, the genitals seem to be in line with a dermatomal continuity, see Dietrich et al., 2017) as first assumptions placed them below the toes in the paracentral wall near the cingulate gyrus (Foerster, 1936; Pfeifer, 1920). Contrary to popular belief, however, the two classical publications by Penfield reported only three cases of genital stimulation out of 400 (Penfield & Jasper, 1954; Penfield & Rasmussen, 1950). Only vague genital sensory sensation and no motor activity or erotic sensation was induced by stimulations in the posterior postcentral gyrus. They described the relation of the genitalia near the toes as unclear and later assumed the genitalia to be represented more laterally than proposed initially. The notion of a more lateral representation was disregarded in the first drawings of the homunculus. Genitalia and rectum were incorporated into drawings according to assumptions (Penfield & Boldrey, 1937). Overall, these studies supported previous work based on animals (de Barenne, 1935; Polyak, 1932) that suggested both pre- and postcentral regions of the human brain could be involved in sensory representations. Later, cortical representations of the rectum were found by Scarff (1940) who described contractions in the rectal sphincter (measured by a physician inserting his finger in the patient's rectum) which were caused by cortical stimulations near the corpus callosum in the medial wall. Another case of genital sensation was reported by Erickson (1945). Although cortical stimulation did not invoke genital sensation, the female epileptic patient suffered from orgasmic seizures and hypersexual episodes accompanied by genital sensations which went beyond just sensory perception of the genitalia and actually lead to erotic feelings. The patient had a tumor at the end of the central fissure between the falx and the medial surface of the right hemisphere and reported her genital sensations to be localized only contralaterally on the left-hand side of her vagina "... just the same as ordinary intercourse, but only on the left side" (Erickson, 1945, p. 229). Similar instances were reported by Kennedy (1959) and also within works without cortical stimulation (Bachman & Rossel, 1984; Ruff, 1980; Terzian & Frugoni, 1958). The contralateral pathways in somatotopy seemed to hold for genitals as well, while Foerster (1936) initially reported bilateral sensations of the genitalia. First sensations beyond the genitalia also involving erotic feelings were induced by Kennedy (1959) through stimulations in the cortical fissure where genitals were assumed to be represented. In this study, the author discussed how stimulations of this area are also related to seizures involving rhythmic movements and sensory experiences related to the autonomic system (e.g., abdominal sensations). This would seem to be the earliest mention of erotic sensations. Both Penfield and Rasmussen (1950) and Foerster (1936) clearly and strictly state the absence of any sexual sensation. However, this could be in part due to a "false sense of modesty" (Penfield & Boldrey,

Table 2 Electrophysiological localization of genitals and sexual arousal in the human brain

Study	Sample		Results
	Female	Male	
Allison et al. (1996)	47 (age range = 10–54)	–	Stimulations in the paracentral lobule inferior to the representations of the foot were associated with sensory perceptions in the penis
Bancaud et al. (1970)	1 (age = 20)	–	Stimulations of posterior hippocampus led to orgasm
Bradley et al. (1998)	–	1 (age = 30)	Stimulations lateral in the postcentral gyrus led to sensory perceptions in the penis
Castelli et al. (2004)	10 (mean age = 60.3, SD = 4.6)	21 (mean age = 62.3, SD = 4.5)	Stimulation of subthalamic nucleus led to higher sexual function
Erickson (1945)	1 (age = 55)	–	Stimulation gave no sensation in vagina but tumor in falx assumed to have led to vaginal sensations contralateral to tumor location
Ferrari et al. (2015)	10	10 (mean age [entire sample] = 22.9, SD = 1.9)	Stimulation of the right dorsolateral prefrontal cortex led to higher ratings of attractiveness for facial stimuli
Foerster (1936)	–	1 (age and gender missing)	Stimulations in the paracentral lobule inferior to the representations of the foot were associated with sensory perceptions in the penis and the anus (itch and sting)
Gloor (1986)	1 (age = 40)	–	Stimulation of right amygdala led to sensation in vulva, feelings of sexual arousal, and autobiographical memories of sexual intercourse
Heath (1964)	–	54 (age and gender missing)	Stimulations of septum led to feelings of sexual arousal and erections
Heath (1972)	1 (age = 34) from Heath (1964)	1 (age = 24) from Heath (1964) same as in Moan and Heath (1972)	Stimulations of the septum led to sexual arousal
Hwynn et al. (2011)	–	10 (mean age [entire sample] = 66.1, gender missing)	Stimulation of the subthalamic nucleus and the globus pallidus internus led to increases in sexual symptoms and improvement of sexual dysfunction (not significant)
Kennedy (1959)	1 (age = 24)	–	Stimulations into the longitudinal fissure (2.5 cm) led to vaginal sensations
Laxton et al. (2010)	1 (69)	–	Stimulation of the right and left hypothalamus (and anterior part of vertical fornix) led to sexual sensation
Merola et al. (2017)	64	86 (age range [entire sample] = 37–70, mean 59.1, SD = 7.2)	Stimulation of the subthalamic nucleus led to a reduction in hypersexuality
Moan and Heath (1972)	–	1 (age = 24) from Heath (1964)	Stimulations of the septum led to sexual arousal
Penfield and Boldrey (1937)	–	1 (age missing)	Stimulations in the paracentral lobule inferior to the representations of the foot were associated with sensory perceptions in the penis (contralateral and no motor response)

Table 2 (continued)

Study	Sample		Results
	Female	Male	
Penfield and Rasmussen (1950)	1 (age = 27)	1 (age missing)	Stimulations in the paracentral lobule inferior to the representations of the foot were associated with sensory perceptions in the penis (and the contralateral buttock)
Portenoy et al. (1986)	1 (age = 48)	–	Stimulation of the posterior postcentral gyrus led to sensations in the left buttock (a glioma in the right postcentral gyrus was associated with seizures involving sensation in the left labium, breast and nipple)
Prause et al. (2016)	15	5 (mean age [entire sample] = 34.6, SD = 10.9)	Stimulation in the right nucleus ventralis posterolateralis led to sexual arousal
Rémillard et al. (1983)	1 (age = 23)	–	Stimulations in the left dorsolateral prefrontal cortex led to higher alpha activity in anticipation and reception of vibratory stimulation in the genitalia
Roane et al. (2002)	–	1 (age = 57)	Stimulations of amygdalohippocampal junction and posterior temporal cortex led to sexual arousal and “good feeling” (p. 324) in lower abdomen
Romito et al. (2002)	–	2 (mean age = 47)	Stimulation in the left globus pallidus led to inappropriate hypersexual behavior
Scarff (1940)	–	1 (age missing)	Stimulation of subthalamic nucleus led to higher sexual drive, sexual interest and inappropriate hypersexual behavior
Serranová et al. (2013)	–	22 (mean age [patients with Parkinson’s disease] = 56.3, mean age [controls] = 54.4)	Stimulation near the corpus callosum beneath the superior boarder of the hemisphere was associated with contractions of the rectal sphincter
Surbeck et al. (2013)	1 (age = 49)	–	Stimulation of the subthalamic nucleus led to higher blink reflex for erotic visual stimuli
Teive et al. (2016)	–	2 (mean age = 64.5)	Stimulations of the hippocampus led to orgasmic seizures
Visser-Vandewalle et al. (2003)	–	2 (mean age = 43.5)	Stimulation of the subthalamic nucleus led to excessive sexual activity
Visser-Vandewalle et al. (2005)	–	1 (age and gender missing)	Stimulations of thalamus (bilateral) led to increased sexual drive and reduced sexual potency
			Stimulation of subthalamic nucleus led to hypersexuality 1 year after the stimulation

Table 3 Neuroelectric reactions toward electric genital stimulation

Study	Sample		Place of stimulation	Results
	Female	Male		
Allison et al. (1996)	18	39 (age range [entire sample] = 10–54)	Dorsal pudendal nerve	Representations of genitalia and perineum assumed in the cingulate sulcus (intracranial recordings)
Bradley et al. (1998)	–	6 (age range = 26–43)	Dorsal nerve of penis	Representations of dorsal nerve of penis afferents assumed in the cingulate sulcus and dorsolateral surroundings (intracranial recordings)
Ertekin et al. (1985)	–	111 (14 controls and 97 patients with impotence and other neuropsychiatric symptoms [age range = 18–65])	Glans penis stimulation	Longer latencies and higher amplitudes for penile SEP compared to peroneal SEP
Fitzpatrick et al. (1989)	–	6 (age range = 24–45)	Dorsal nerve of penis	N90 showed higher decrease during repeated self-stimulation of dorsal nerve of penis than self-stimulation of posterior tibial nerve
Guérit and Opsomer (1991)	5	5 (age range [entire sample] = 24–48)	Dorsal nerve of penis and clitoris	Smaller field gradients for penile and clitoral stimulations than for stimulations of the posterior tibial nerve
Haldeman et al. (1982a)	7 (age range = 20–40)	13 (age range = 20–40)	Dorsal nerve of penis and clitoris	Male cortical pudendal evoked responses were twice the size of the female pudendal evoked responses and cortical evoked response of the dorsal nerve of the penis was maximal at Cz
Haldeman et al. (1982b)	–	10 (7 controls: age range = 25–60, 3 lesion patients: mean age = 56.33)	Dorsal nerve of penis	Compared to healthy controls, a lesion patient showed higher latencies for the bulbocavernosus reflex (patient had also erectile dysfunction) and an absence of cortical responses to stimulations of the pudendal nerve
Opsomer et al. (1986)	10 (age range = 20–34, median = 26)	10 (age range = 20–32, median = 25)	Dorsal nerve of penis and clitoris	Earlier onset of response in women and higher amplitude in men
Stowell (1983)	2	1 (age range [entire sample] = 22–59)	Perineum	Perineum stimulation resulted in longer latencies than stimulation of big toe
Yang and Kromm (2004)	77 (age range = 19–49)	–	Dorsal nerve of clitoris	Larger amplitude and longer latencies for stimulations of the dorsal nerve of the clitoris compared to perineal nerve stimulations

Table 4 Neuroelectricity related to orgasms and genital arousal

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Cohen et al. (1976)	3	4 (age range [entire sample] = 21–32)	One group performs masturbation in 3 phases (prelimax 15 min without physical stimulation, actual masturbation till 1 or more orgasm, postclimax resting period 15 min)	Manual self-stimulation till orgasm	ERP (visual inspection)	Fantasying about sexual imagery or erotic films and pictures (only for 2 subjects) during preclimax	Higher increase in right-hemispheric than in left-hemispheric amplitude during orgasm compared to preclimax
Cohen et al. (1985)	–	18 (age range = 31–60, mean age = 46.1)	Three groups (6 high responders to erotic stimulation [average age = 45, age range = 37–57], 6 low responders to erotic stimulation [average age = 47, age range = 32–60], 6 sexually dysfunctional men [average age = 46.2, age range = 31–56]) watch 2 different visual stimuli and listen to 2 different auditory stimuli	Passive viewing and listening	ERP	Erotic videos without sound and auditory description of sexual activity	<i>R/L</i> ratios showed more right-hemispheric activity (temporal) and maximum penile tumescence during erotic video than during neutral video only in the high responder group
Graber et al. (1985)	–	4 (age range 20–24)	Four subjects perform masturbation	Manual self-stimulation till orgasm	ERP (visual inspection)	–	Decrease in alpha activity during orgasm
Heath (1972)	1 (age = 34) from Heath (1964)	1 (age = 24) from Heath (1964) same as in Moan and Heath (1972)	One patient performs task	Orgasmic response (masturbation, intercourse or chemical induction)	ERP (visual inspection)	Introduction of acetylcholine and levaterenol bitartrate in septal regions, prostitute, or erotic film	Intracranial recordings from septal sites showed spikes, fast high-amplitude spindles, and slow-wave activity during orgasm

Table 4 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Hirshkowitz et al. (1984)	–	12 (age missing)	One group performs task with 3 different film categories	Passive viewing and sleep	qEEG	Erotic films	Phases of maximal nocturnal penile tumescence showed enhanced EEG asymmetry (more right than left activity) in temporal sites (T3–CZ and T4–CZ)
Moan and Heath (1972)	–	1 (age = 24) from Heath (1964)	One patient performs task	Sexual intercourse	ERP (visual inspection)	Prostitute	Intracranial recordings from septal sites showed increase in delta waves, fast superimposed frequencies, spikes and slow-wave activities (resembling seizures) immediately prior and during orgasm
Mosovich and Tal-lafarro (1954)	3	3 (age range [entire sample] = 23–38)	One group performs masturbation in 3 phases (erotic stimulation, orgasm and phase after ejaculation)	Manual self-stimulation till orgasm	ERP (visual inspection)	Fantazising about sexual imagery	Increase in low-voltage rapid activity (temporal areas) during erotic stimulation, increase in voltage and slowing of the electrical activity during orgasm, low-voltage rapid activity after ejaculation
Ponseti and Bosinski (2010)	–	20 (mean age = 25.9, SD = 5.2)	One group performs task with 1 set of pictures	Passive viewing	ERP	Erotic pictures	Erection-related EEG activity was associated with electrical activity of the corpus cavernosum
Ponseti et al. (2009)	–	20 (mean age = 25.9, SD = 5.2)	One group performs task with 1 set of pictures	Passive viewing	ERP	Erotic pictures	EPN was associated with penile erection and maintenance, while P3 was associated with penile detumescence

Table 4 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Radilová et al. (1983) (abstract); Study 2	–	16 (age range = 19–29, mean age 23.3)	One group performs task in 2 different emotional states	Passive viewing of erotic pictures till erection and viewing of geometrical figures (number of squares) during erection and without erection	ERP	Erotic pictures	P300 (occipital region) during viewing of geometrical figures was lower during state of erection than without erection
Rosen et al. (1986)	–	20 (age range = 23–35, mean = 29.3, SD = 3.6)	One group performs task	Sleep	qEEG	–	Phases of maximal nocturnal penile tumescence showed enhanced EEG asymmetry (more right than left activity) in C3–C4 and A1–A2
Sarrel et al. (1977)	1 (gender and age missing)	–	One subject performs masturbation	Manual self-stimulation till orgasm	ERP (visual inspection)	–	Observable change in scalp EEG through orgasm (not specified)

1937, p. 418) on the patient side preventing them from reporting sexual sensations. Another reason could be the author's biases toward an overly inoffensive and politically correct procedure (Di Noto, Newman, Wall, & Einstein, 2013). Especially in the one female patient (Penfield & Rasmussen, 1950), the repeated emphasis of an absence of any sexual arousal (with italic letters) is striking.

Further cortical stimulation experiments later supported the notion that the genitalia are represented more laterally in the postcentral gyrus than initially assumed and adjacent to sensory areas for the abdomen (Bradley, Farrell, & Ojemann, 1998). It was theorized that the dorsal nerve of the penis consists of exclusively afferent fibers that project to a large area of the primary sensory cortex with a conduction time of 27–30 ms (Bradley et al., 1998). Others placed the genitalia more anterior to the foot region near the cingulate sulcus (Allison, McCarthy, Luby, Puce, & Spencer, 1996; for a review, see Parpia, 2011). If localized within the cingulate sulcus, it could explain the rare encounters of genital sensations (Allison et al., 1996).

A potentially more detailed description of the locality of cortical regions responsible for feelings of sexual arousal instead of genitalia was reported in a series of experiments performing intracortical stimulations for therapeutic purposes in 54 patients (Heath, 1964, 1972; Moan & Heath, 1972). Out of various brain regions, only stimulations of the septal region repeatedly led to self-reported sexual arousal and in some cases even to erections but no orgasms. Based on studies on rats (e.g., Olds & Milner, 1954), this region was assumed to be a pleasure center. In one epileptic patient with sexual seizures, stimulations of the posterior hippocampus with propagation to the amygdala and the temporal cortex lead to orgasms and sensations resembling the patient's spontaneous seizures (Bancaud et al., 1970). Gloor (1986) similarly describes an epileptic case where stimulation of the right amygdala leads to a pleasant feeling in the female patient's vulva apart from an abdominal feeling of nausea. The feeling was described as having sexual intercourse without actually seeing the partner but knowing him to be her late and first sexual partner. In this patient, stimulation of the right amygdala with a discharge in the limbic structures of the right temporal lobe and temporal neocortex triggered feelings of sexual arousal related to autobiographical memory and were again described as similar to her spontaneous seizures. In a similar case (stimulation in the hypothalamus) again sexual sensations were reported involving autobiographical relations (Patient 2: Laxton et al., 2010). Further neurosurgical reports in patients with sexual seizures found feelings of sexual arousal triggered by stimulations in the amygdalohippocampal junction, with one patient reporting a “good feeling” in the lower abdomen combined with sexual arousal when stimulations were carried out in the posterior temporal cortex (Rémillard et al., 1983, p. 324). Orgasmic ecstasy was

also induced in an epileptic patient through stimulation of the hippocampus with a discharge spreading to the parahippocampal gyrus, the insula, and the temporal lobe (Surbeck, Bouthillier, & Nguyen, 2013). In all such cases, the sexual experiences induced were momentarily and not mistaken for real events unlike in hallucinations. In some instances, these results were related to works on the visual modality where connections from the visual cortex were shown to be anteriorly directed through a ventral course and channeling visual information through the inferior temporal neocortex (Mishkin, Lewis, & Ungerleider, 1982; Mishkin & Ungerleider, 1982). This system was assumed to retain visual objects in memory. In one patient that was treated for chronic pain syndrome, self-stimulations through an electrode placed in the right nucleus ventralis posterolateralis (deep brain stimulation [DBS]) produced erotic sensations without orgasms (Portenoy et al., 1986). This led to the patient frequently self-stimulating even neglecting other commitments or hygiene. It was assumed that these stimulations could have led to altered metabolic functions in the nearby thalamic structures triggering compulsive self-stimulations similar to addict behavior. Only two studies were found using less invasive means of cortical stimulation in relation to human sexuality. Prause, Siegle, Deblieck, Wu, and Iacoboni (2016) used transcranial magnetic stimulation (TMS) of the left dorsolateral prefrontal cortex (L-DLPFC) and influenced brain waves, detected by EEG, in anticipation and during reception of vibratory stimulation in the genitalia. This effect was absent when monetary reward was anticipated or received. Transcranial direct current stimulation (tDCS) of the right DLPFC influenced the perception of attractiveness of facial stimuli in another study (Ferrari, Lega, Tamietto, Nadal, & Cattaneo, 2015). The effects of the noninvasive stimulations also lasted only through short experimental sessions. The findings were interpreted with the causal role of the DLPFC in judgments of facial attractiveness and it is linked to the dorsal anterior cingulate cortex' function of upregulating sexual responses.

Longer-lasting effects on sexual behavior through electrical stimulation in the brain have been reported after surgery in studies using modern DBS. One case involved hypersexual behavior 1 year after surgery in a Parkinson patient that has received stimulation in the subthalamic nucleus (Visser-Vandewalle et al., 2003, 2005). Such stimulations were also linked to higher sexual functioning predominantly in males younger than 60 years (Castelli et al., 2004, although in one explorative study stimulation of the subthalamic nucleus was not associated with hypersexuality Hälbig et al., 2009) but also in two cases older than 60 (Teive, Moro, Moscovich, & Munhoz, 2016). The increase in sex drive and sexual interest even led to inappropriate and indiscriminate seductive behavior toward medical staff in one case (Romito et al., 2002). In another study on Parkinson's disease, slight increases in sexual symptoms and improvement of sexual dysfunction were

observed, albeit neither to a statistically significant degree, after stimulation of the subthalamic nucleus or the globus pallidus internus (Hwynn et al., 2011). In a recent study with a larger sample stimulation of the subthalamic nucleus led to significant reduction in hypersexuality as assessed with clinical interviews (Merola et al., 2017). Stimulation of the subthalamic nucleus also led to a larger acoustic blink reflex for erotic visual stimuli when compared to a condition without stimulation or to a matched control group also without stimulation (Serranová et al., 2013). Only erotic and neither food nor aversive stimuli resulted in higher reactions in the stimulation condition compared to both other conditions (Serranová et al., 2013). The left globus pallidus was also linked to hypersexual and inappropriate behavior (e.g., frequent sexual remarks to strangers or younger female relatives) in a patient suffering from Parkinson's disease who received stimulation in that region (Roane, Yu, Feinberg, & Rogers, 2002). In a larger sample of cases with stimulations both in the subthalamic nucleus and in the globus pallidus, hypersexual aftereffects (assessed with questionnaires and not further specified) seemed more frequent in the group with stimulations in the globus pallidus; however, in both groups such cases were very rare (Hariz, Rehnroona, Quinn, Speelman, & Wensing, 2008). A similar comparison of two such groups (stimulation in subthalamic nucleus and stimulation in globus pallidus) showed no difference between the two groups in erectile dysfunction but a trend for deterioration when both groups were analyzed for poststimulation outcomes (Mock et al., 2016). In one Tourette patient, bilateral stimulation of the thalamus led to increased sexual drive while another experienced reduced sexual potency (Visser-Vandewalle et al., 2003). Both patients also experienced changes in erectile function according to their behavioral alterations (Temel et al., 2004). Such observations were explained with the association between mood and the subthalamic nucleus and the globus pallidus. Alterations in the globus pallidus could change the circuitry in the medial orbitofrontal-basal ganglia which is involved in the regulation of sexual behavior (Zald & Kim, 2001). Stimulation of the subthalamic nucleus on the other hand directly affects limbic-related regions, e.g., anterior cingulate gyrus (Limousin et al., 1997).

Neuroelectric Reactions Toward Electric Genital Stimulation

Instead of stimulating the cortex invasively, electrical stimulation can also be induced in the genital area while electrical scalp potentials are recorded. The preferred method in studies with genital stimulation (Table 3) involved combinations of somatosensory evoked potentials (SEPs; i.e., electrical or non-electric stimulation of the periphery and simultaneous recording of ERPs either at the scalp or in-depth) from mostly healthy participants. Two studies used intracranial recordings of SEPs in epileptic patients (Allison et al., 1996; Bradley

et al., 1998). The studies on genital stimulation focus on ERP components. In the corresponding studies, usually multiple EEG segments were averaged around an event of interest and compared to averaged waves of other events or conditions. ERPs are assumed to reflect the electric response in the brain toward the event of interest in a time-contingent way. Within such an average waveform, the peaks are named according to their voltage (positive or negative, abbreviated as P or N, respectively) and their timely order. Consequently, the first negative peak would be labeled N1 by this convention. Usually, latencies and peak amplitudes of components are used for statistical comparisons. Using such methods, the goal was to measure nerve velocities, evaluate the somatosensory pathways of the genitals, or to develop electrodiagnostic tools for sexual function.

Genital stimulation often results in SEPs with longer latencies, when compared to stimulations from other nerves and body parts. Using SEPs in patients with intractable epilepsy, Allison et al. (1996) suggested representations of the genitalia and perineum in the cingulate sulcus (anterior to the foot sensory area). This was based on intraoperatively central-side recordings of evoked responses (effects in P40) by stimulation of the dorsal pudendal nerve (electrodes placed on penis or clitoris) resulting in a “warm tingling sensation” (p. 133). Similar responses have been described with initial stable positive deflections (P1) and more variable subsequent waves as well as larger overall amplitudes in males (0.5–2 μ V) than in females (0.2–1 μ V; Haldeman, Bradley, Bhatia, & Johnson, 1982a). Although longer latencies and more posterior distributions (N45, P56) have been observed for penile than for clitoral stimulations, this outcome may have been confounded by gender differences in body size (Guérit & Opsomer, 1991). Stimulations of the dorsal penile nerve also resulted in similar SEPs as stimulations of the much longer posterior tibial nerve (Haldeman et al., 1982a) as well as the peroneal nerve (Ertekin, Akyürekli, Gürses, & Turgut, 1985). In contrast, one study found smaller amplitudes for penile and clitoral stimulations than for stimulations of the posterior tibial nerve (Guérit & Opsomer, 1991). Differences between genital stimulation and posterior tibial nerve stimulations were found in P38 (latency) in P30, P38, and P56 (field gradients) (Guérit & Opsomer, 1991). A more recent study used advanced electrodiagnostic methods and replicated the clinical significance of the P1 in genital stimulation as well as the longer latencies and larger amplitudes for clitoral SEPs compared to perineal nerve SEPs (Yang & Kromm, 2004). Interestingly, perineum stimulations also resulted in longer latencies than stimulations of the big toe (Stowell, 1983). Longer SEP latencies for bulbocavernosus reflexes were further observed in patients with diabetic impotence while penile SEP was more influenced by spinal cord injury and parkinson (Ertekin et al., 1985). In multimorbid

samples, neurodegenerative disorders appeared to influence genital SEPs (Ertekin et al., 1985).

Apart from results reduced to amplitude and latency, some experiments have depicted a high sensitivity of genital nerves and a variety of cortical structures involved in sexual arousal and orgasm. Studies on sensation showed that the percutaneous stimulation of the penis leads to a more precise sensation of locality with more discrete perception of differences in stimulation compared to stimulations of other body parts (Stowell, 1983). There was also a greater amplitude decrease in the dorsal penile nerve than in posterior tibial nerve when self-stimulated (Fitzpatrick, Hendricks, Graber, Balogh, & Wetzel, 1989). The N90 was further sensitive to stimulation repetition and prior knowledge of stimulation with both factors leading to a decrease in amplitude (Fitzpatrick et al., 1989).

The clinical value of such stimulations for sexual function has been called into question (Delodovici & Fowler, 1995; for a review on other clinical applications, see Bianchi et al., 2017), and it has been noted that electrical stimulations lead to activations of larger brain regions than other stimulations (Forss, Salmelin, & Hari, 1994; Kell, 2005). The studies reviewed here show how sensations mediated through genital nerves can be recorded through brain potentials and related to the integrity of the somatosensory pathways. Less evidence was shown for a continued cortical grouping of neurons responding to a specific stimulus (e.g., Bradley et al., 1998). Genital stimulation was also mostly studied without experimentally targeting sexual arousal.

Neuroelectricity Related to Genital Arousal and Orgasm

In some studies, genital nerves were not stimulated electrically. Instead, the subjects were instructed to manually stimulate themselves, sometimes till orgasm, while EEG was recorded (Table 4). At the time of the earliest studies reviewed in this section, the technical means to store EEG data for quantifications were not available and analysis relied solely on visual inspection. Later studies started calculating ERPs, sometimes also used quantifications of hemispheric asymmetries in EEG (qEEG) and resemble more modern neuroscientific studies with experimental designs involving different conditions and tasks. At times, studies did not provide subjects with erotic material for stimulation and only few studies related EEG results to behavioral data or questionnaires. Based on prior phenomenological reports, orgasm was theorized to be a very unique state of consciousness comparable with a loss of touch with immediate reality and maybe even similar to feelings of dying (Keiser, 1952). EEG was used in an attempt to quantitatively describe this state.

First EEG recordings during orgasm were described by Kinsey, Pomeroy, Martin, and Gebhard (1953) by citing preliminary results from later published work by Mosovich

and Tallafiero (1954) who asked their subjects to masturbate, while 1-h-long EEG recordings were taken. Increases in slow activity and high voltage were observed at the temporal sites and spread from there. These observations led to the first comparisons of brain waves during orgasm to brain waves during epileptic seizures (Kinsey et al., 1953; Mosovich & Tallafiero, 1954). Similarities between epileptic seizures and orgasm were already noticed by Democritus (as cited in Kinsey et al., 1953) through behavioral observation only. Mosovich and Tallafiero (1954) theorized that not only genital areas are involved in sexual responses, but also other cortical and subcortical structures associated with autonomic functions.

Intracranial recordings from septal regions during orgasm were later also compared to epileptic discharges (Heath, 1972; Moan & Heath, 1972). In these studies, orgasm was induced by either chemical induction in the septal region (acetylcholine or levarterenol bitartrate) in a female subject or by self-stimulation till orgasm during an erotic film or intercourse with a prostitute in a male subject. Orgasms showed spikes, increase in delta waves, fast superimposed frequencies and slow activities (with frequencies of 1.5–2 s). While Mosovich and Tallafiero (1954) attempted to identify muscle artifacts, no such controls were made in Heath (1972) and Moan and Heath (1972). The focus on the septal region was again based on previous animal studies showing that this region is involved in experiences of pleasure (Olds & Miller, 1954). Although later case studies on brain injury also linked this region to sexual function in humans, it was always in combination with other diencephalic or basal-frontal regions (Miller, Cummings, McIntyre, Ebers, & Grode, 1986).

Introducing a portable device using a cassette recorder to sample EEG data during sexual activity, Sarrel et al. (1977) reported EEG recordings during an orgasm but did not go into any specifics about the results. Also, the apparatus was not used in later research. Further attempts at reducing movement artifacts were made in Cohen, Rosen, and Goldstein (1976). Although none of the studies mentioned so far compared control groups to masturbation, Cohen et al. did instruct a participant to fake orgasm and another one to use the left hand instead of the right to compare differences. Without modern methods of artifact reduction, Cohen et al. tried to select artifact-free segments for analysis. A higher right-hemispheric than left-hemispheric activity during orgasm was reported by that group. This was determined with amplitude measures, specifically a change in *R/L* (right/left) amplitude ratios (at parietal sites), with one subject showing also a 10-Hz pattern left and 4-Hz on the right during orgasm compared to the prelimax phase. This marked the first findings on hemispheric EEG asymmetries in relation to human sexual arousal on which a large number of later studies focused on. While some replicated this asymmetry with different experimental procedures (Cohen et al., 1985)

and in sleep studies recording EEG during nocturnal penile tumescence (Hirshkowitz, Karacan, Thornby, & Ware, 1984; Rosen et al., 1986), another study found only a nonspecific decrease in alpha activity during orgasm (Graber, Rohrbaugh, Newlin, Varner, & Ellingson, 1985). Nevertheless, sexual orgasm was interpreted as a unique state of consciousness with a dissociation between the left and right EEG suggesting a predominant change in the right hemisphere. In one further study, erection reduced the P300 response toward pictures of geometrical figures as compared to viewing without erection (Radilová et al., 1983, second study) hinting at an effect of erection on selective attention.

So far, only a few studies looked at EEG activity during erection and orgasm and some inconsistencies require further research. The risk of contaminating movements and the choice of the appropriate time windows to sample erections and orgasms in isolation are challenges to this day. A more recent study has employed more sophisticated technical equipment and statistical analysis on simultaneous recordings of penile tumescence and EEG in awake participants and ascribed different EEG epochs to different stages of penile tumescence using independent component analysis (Ponseti, Kropp, & Bosinski, 2009). Erection and maintenance of erection were more strongly related to early posterior negativity (EPN), while detumescence was more closely related to the P3 component. This early EEG activity during erection was further correlated with electrical activity in the corpus cavernosum of the penis during that stage (Ponseti & Bosinski, 2010). These studies demonstrate how the corpus cavernosum receives autonomous signals already after early preattentive cognitive processing of sexual pictures.

Cognition and Sexual Arousal

The largest number of studies looking at neuroelectric signals elicited by erotic stimulation consists of typical experiments in laboratory settings with a focus on cognitive neuroscience (Table 5). The primary goal here was to investigate how any form of erotic stimulation influenced electrical signals on the scalp and cognitive functions in healthy participants. Most of the studies in question were conducted without focusing on physiological genital arousal or orgasm. Instead, the corresponding studies relied on visual, auditory, or olfactory means (or a combination of those modalities) in order to elicit erotic stimulation (for a review on visual sexual stimuli, see Gola et al., 2016). Simultaneous, healthy participants would perform a cognitive task or simply perceive the stimulation passively.

EEG offers multiple ways to extract signals for statistical inference. Apart from the usual ERP components (N1, P1, N2, etc.), other established components provide useful research tools and have been widely utilized within the following studies (e.g., late positive component: LPC; late

positive potential: LPP). The mismatch negativity (MMN; Näätänen, Gaillard, & Mäntysalo, 1978) is an ERP component assumed to represent violations to sensory regularities of visual or auditory modalities, for instance. Neuroelectric responses to violations of visual sensory regularities have been investigated with numerous studies using emotional visual stimuli, preferably faces (Csukly, Stefanics, Komlósi, Czigler, & Czobor, 2013; Fujimura & Okanoya, 2013; Kimura, Kondo, Ohira, & Schröger, 2012; Kreegipuu et al., 2013). The MMN has less commonly been used in ERP studies with sexual stimuli. Another relevant component is the contingent negative variation (CNV; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV is assumed to represent cognitive anticipation and expectation toward a stimulus and has also been investigated with emotional stimuli (Eimer & Holmes, 2007; Gan, Wang, Zhang, Li, & Luo, 2009). Besides ERPs, EEG allows for methods involving transformations of EEG waves into frequency domains. In this way, the frequencies of waves (e.g., alpha, beta) can be compared between experimental conditions. These measurements, also referred to as quantitative EEG (qEEG), are often used on recordings over longer durations where EEG is assumed to be stationary. There are also numerous ways to calculate coherence between different electrode sites to make assumptions about similar oscillatory activity between them. Other methods record scalp potentials and then use source reconstruction to localize the source within the brain responsible for those scalp potentials (current source densities). These multiple ways to analyze EEG data allow for highly variable experimental procedures. As the electrophysiological studies conducted with regard to cognition and sexual arousal reflect this wide array of methodology, it is difficult to compare the results of different studies from this area. Another strand of research comprises analyses of the way in which EEG measurements, affected by sexual stimulation, are possibly related to behavioral data indicative of sexuality (e.g., performance measures in tasks with sexual stimuli, such as response accuracy or reaction time, RT). Other behavioral correlates include subjective ratings of stimuli (e.g., ratings of erotic pictures as sexually attractive) or self-reports of sexual preference or sexual arousal. Compared to such measures, EEG data can either mirror or complement the behavioral data.

Over 50 years ago, Cohen and Walter (1966) observed how “intrinsically interesting pictures” (p. 194: semi-nude females for male subjects) elicited larger amplitudes than geometrical forms. First EEG experiments on sexual stimuli were done by Lifshitz (1966) who showed different picture categories including female nudes to an all-male sample while recording EEG. The participants were merely instructed to view the images passively. The ERPs were compared qualitatively through visual inspection. According to Lifshitz, differences between the ERPs toward female

nudes as compared to all the other stimuli became visible. These findings were referenced by Costell, Lunde, Kopell, and Wittner (1972) who was interested in how the ERPs would manifest itself if sexual stimuli matched own sexual preference compared to sexual stimuli without such a match. Therefore, the sample comprised both male and female participants as well as images of female and male nudes. They assumed that preferred sexual stimuli would lead to a more pronounced CNV when compared to non-sexual and non-preferred stimuli. The results showed higher CNV to opposite-sex nudes than to same-sex nudes for participants of either gender. Higher CNV in anticipation toward erotic pictures were triggered if the erotic pictures were announced either by pictures (Costell et al., 1972) or simply by tones (Simons et al., 1979). Using appropriate experimental designs, results could be interpreted as anticipatory effects and not motoric preparations for task performances (Simons et al., 1979). Tones predicting the display of erotic pictures also triggered higher P3, while this effect was almost absent in anhedonic participants (Simons, 1982). The P3 was also larger toward erotic pictures without anticipation effects when compared to a series of other pictures with neutral (e.g., landscapes), positive (e.g., toddlers and flowers), or negative (e.g., dermatological) content (Johnston, Miller, & Burleson, 1986; Miller, 1985; Radilová et al., 1983). It was postulated a subjective value hypothesis (Johnston et al., 1986; Miller et al., 1986). The assumption was that all ascribed value to stimuli would be emotive in nature. Based on inherent emotions, a stimulus will be defined as either desirable or undesirable for survival. The emotional value ascribed can be inferred from the P3 amplitude. Effects of erotic stimuli were also shown on later positive components (P4; Johnston et al., 1986). These results on the P3 as well as the P4 were the same when averaged peak values were used (Johnston, Burleson, & Miller, 1987) or when the components were extracted using principal component analysis (PCA: Wood & McCarthy, 1984) on the ERPs (Johnston et al., 1986). On average, the P3 was reduced toward neutral pictures when erotic pictures had been shown prior to the neutral ones (Radilová et al., 1983). Thus, initial findings showed higher ERP amplitudes for sexual pictures than for non-sexual pictures of positive and negative content. Moreover, higher ERP amplitudes for sexual pictures were recorded if the sexual content matched the sexual preference of the subject.

Later studies replicated the results on the P3 (Johnston & Wang, 1991; Schupp et al., 1996), the CNV (Howard, Longmore, & Mason, 1992; Howard, Longmore, Mason, & Martin, 1994), or later positive components (Poli, Sarlo, Borroletto, Buodo, & Palomba, 2007, but see Carretié, Iglesias, García, & Ballesteros, 1997 with no effect of erotic pictures on the P300 and N300). The same held for stimuli involving facial attractiveness (LPC; Johnston & Oliver-Rodriguez, 1997). When facial proportions were modified to make faces

Table 5 Cognition and sexual arousal

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Alexander and Sufka (1993)	10 (mean age missing)	14 (age missing [entire sample])	Three groups (heterosexual males, heterosexual females) perform 2 tasks	Verbal and spatial task and a baseline condition akin to a resting state EEG (affective judgments also required)	qEEG	–	Baseline: higher asymmetry (alpha, F1, F2, T7, T8, P3, P4, O1, O2) in homosexual males than in heterosexual males and females Verbal task: higher alpha activity (F1, F2, T7, T8, P3, P4, O1, O2) in homosexual males than heterosexual males but not than heterosexual females
Alho et al. (2015)	9	9 (mean age [entire sample]=24.4, SD=4.0)	One group performs task with 4 different picture categories	Detection task	ERP, source localization	Erotic pictures (attractive nude bodies)	Higher N1 (T5, T6) and longer latencies to nude compared to clothed bodies. Compared to clothed bodies, naked bodies elicited stronger early activity in ventral temporal cortex, lateral occipitotemporal cortex and late activity in ventral temporal cortex, lateral occipitotemporal cortex, insular, lateral orbitofrontal, and anterior cingulate cortex
Amezcu-Gutiérrez et al. (2016)	–	69 (age range=25–35)	Three groups (each N=23) perform task after watching 3 different films	Passive viewing, rating task (right after watching film) and Tower of Hanoi Task after film	qEEG	Erotic film (scenes from movie “Cat Woman”)	The erotic group showed an increased parietal interhemispheric correlation (P3, P4) in the slow delta and theta band, and a decrease in prefrontal delta band (F3–F4) during performance of the Tower of Hanoi task Increased frontal intrahemispheric correlations (F3, T3) in the theta band during performance of the Tower of Hanoi task

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Anokhin et al. (2006)	272 (age range = 18–28)	–	One group performs task involving 4 picture categories	Passive viewing (with acoustic startle stimulus)	ERP	Erotic pictures or partially unclothed heterosexual couples in erotic embraces” p. 175)	Erotic pictures were differentiated from positive (non-erotic), negative and neutral pictures at P2, N4 and LPP (Fz, Cz, Pz)
Bailey et al. (2012)	20	20 (mean age [entire sample] = 20.45, SD = 2.55)	One group performs one task with 9 different picture categories	Rating task	ERP	Erotic pictures (erotic heterosexual couples)	More pronounced P2, EPN, and LPP for erotic pictures compared to positive, neutral, negative, and violent pictures
Bartholow et al. (2010)	25	22 (age range [entire sample] = 18–22)	Sample is split into 2 groups (high-sensitivity [HS], low-sensitivity, [LS]) with respect to their alcohol tolerance, and both groups perform a task with 5 different picture categories	Visual oddball task and picture categorization	ERP	Erotic pictures (“men and women kissing; partial nudity”)	Partial least squares analysis on ERP highlighted the difference between erotic and the other picture categories Higher P3 for erotic pictures than for neutral pictures or pictures with alcoholic or non-alcoholic beverages
Briggs and Martin (2008): Study 1	19 (age range = 18–35, mean = 19.89, SD = 4.07)	–	One group performs task with 4 different picture categories	Localization task with peripheral cue	ERP	Erotic pictures (sexual or erotic couples)	Larger P3b amplitude for sexual pictures than for mutilations, threatening pictures, and neutral pictures
Briggs and Martin (2008): Study 2	18 (age range = 18–36, mean = 21.32, SD = 4.46)	–	One group performs task with 4 different picture categories	Target identification task	ERP	Erotic pictures (sexual or erotic couples)	Largest P1 for sexual pictures and larger P3b amplitude for sexual than for threatening pictures and neutral pictures (not differentiated from mutilations at P3b)
Briggs and Martin (2009)	17 (age range = 18–33, mean = 22.06, SD = 4.76)	17 (age range = 18–36, mean age = 21.06, SD = 5.73)	One group performs task with 8 different picture categories	Oddball task (rating task after main task)	ERP	Erotic pictures (erotic couples)	Higher P3b amplitude for neutral, pleasant or unpleasant pictures

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Carretié et al. (1997)	24	8 (age range [entire sample]=19–24, mean =20.91, SD =1.25)	One group performs task with 4 different picture categories	Visual discrimination task (rating task months after main task)	ERP	Erotic pictures (nude model)	Higher N300 amplitude (P3, P4) for erotic than for decomposing bodies, landscapes or buildings (only reported as an interaction between stimulus category and site and not as main effect of stimulus category)
Carvalho et al. (2011)	15 (mean age =21, SD =2)	15 (mean age =24, SD =3)	One group performs task during 5 different film categories	Auditory oddball task during passive viewing of task irrelevant videos (rating task right after film)	ERP	Erotic film (sexual intercourse but no genitalia)	The P3 (300–400 ms, Cz) following the auditory stimulus could not differentiate the erotic film category from all the other categories in any analysis
Chen et al. (2012)	7	7 (age range [entire sample]=19–23, mean =21.9)	One group performs task with 2 different picture categories	Modified trust game	ERP	Erotic pictures (attractive faces)	During face perception, there was a smaller P2, a larger N2 and LPC amplitude for attractive compared to unattractive faces
Codispoti et al. (2006)	26	24 (age range [entire sample]=22–34)	One group performs task with 3 different picture categories	Rating task	ERP	Erotic pictures (erotic couples)	During feedback, there was a larger FRN for attractive than for unattractive faces
Codispoti et al. (2007)	12	12 (age range [entire sample]=21–28)	One group performs task with 3 different picture categories	Passive viewing	ERP	Erotic pictures (erotic couples)	Higher LPP for erotic pictures than neutral pictures (no difference between erotic pictures and mutilations). After 60 repetitions, the effect of erotic pictures and mutilations was still present in the LPP
							More pronounced early potentials (150–300 ms) for erotic and unpleasant pictures compared to neutral pictures
							More pronounced LPP for erotic and unpleasant pictures across blocks

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Costell et al. (1972)	12	12 (age range [entire sample] = 18–22)	Two groups (males and females) perform task with 3 different picture categories	Passive viewing and rating (after main task)	ERP (CNV)	Erotic pictures (nude females, nude males)	Higher CNV (vertex) for opposite-sex nudes than for neutral or same-sex stimuli (both sexes) and higher CNV (vertex) for same-sex nudes than for neutral stimuli (only females)
De Cesarei and Codispoti (2011)	10	10 (age range [entire sample] = 21–30, mean = 24.1, SD = 2.59)	One group performs task with 9 different picture categories	Recognition task (only instructed)	ERP; qEEG	Erotic pictures (erotic couples, male and female nudes)	Erotic pictures (erotic couples as well as opposite-sex nudes) showed higher LPP (CP3, CP1, CPz, CP2, CP4, P3, P1, Pz, P2, P4) than babies, neutral animals, faces, people, animal or human attacks (but not compared to mutilated bodies)
De Cesarei and Codispoti (2006)	8	8 (age range [entire sample] = 20–29, mean = 22.7, SD = 2.27)	One group performs task with 3 different picture categories	Categorization task (animal or person)	ERP	Erotic pictures (erotic couples)	Erotic pictures (erotic couples as well as opposite-sex nudes) showed higher alpha desynchronization (P7, P5, P3, P1, P2, P4, P6, P8, PO7, PO5, PO3, PO2, PO4, PO6, O3, O1, O2, O4) than babies, neutral animals, faces, people, but not animal or human attacks or mutilated bodies
Del Zotto and Pegna (2017)	12	12 (mean age [entire sample] = 25.6)	Two groups (men and women) perform task with 8 different picture categories	Visual oddball task	ERP	Erotic pictures (animated nude bodies)	Early amplitude (150–300 ms) differentiated between erotic and all other pictures and LPP amplitude was larger for erotic than neutral (but not unpleasant) stimuli
							Nude stimuli produced a higher P2 and LPP amplitude than clothed stimuli

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Demidova et al. (2014)	32	14 (age range [entire sample]= 18–21)	Two groups (women and men) perform task with 4 different picture categories	Passive viewing (rating task right after task)	qEEG	Erotic pictures (not specified)	Nude stimuli were associated with earlier P1 latency and the waist-to-hip ratio of the pictures affected the P1 amplitude in the male group and the LPP amplitude in the entire sample Nudity and waist-to-hip ratio affected the N190 amplitude, and the waist-to-hip ratio also affected the N190 latency Men: decrease in alpha and low-frequency beta and increase in high-frequency beta (occipital, parietal and central) when viewing erotic pictures. Increase in beta in left anterior temporal site Women: increase in beta (symmetrical) in temporal (posterior) and occipital sites. Decrease in alpha and theta right temporal (T4) Highest LPP for erotic pictures compared to neutral and cigarette-related pictures (centroparietal sites)
Deweese et al. (2016)	36	37	Three groups (non-smokers [N = 30, 21 females, mean age = 33, SD = 1.7], deprived smokers [N = 21, 7 females, mean age = 41.9, SD = 2], non-deprived smokers [N = 22, 8 females, mean age = 45.9, SD = 2.9]) perform task with 3 different picture categories	Conditioning task and rating task	ERP	Erotic pictures (erotic couples)	

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Dimpfel et al. (2003)	40	40 (mean age [entire sample]=49, SD=9)	Two groups (female and male) perform task with 5 different film categories	Passive viewing	qEEG, source localization	Erotic films (an erotic film ("more or less undressed women in different erotic dance like movements" p. 193), and a sex film ("scenes of various sexual behaviour" p. 193) were used)	Males: During the erotic film subjects showed frontocentral decreases in delta and theta activity and decreases in alpha and beta activity in temporoparietal areas. During the sex film subjects showed decreases in delta and theta activity in frontocentral areas and a decrease in alpha and beta power
Dong et al. (2010)	10	9 (age range [entire sample]=18.4–26.6, mean age=22.1)	One group performs 2 tasks with 2 different picture categories	Rating and false rating	ERP	Erotic pictures (attractive faces)	Females: During erotic film subjects showed more activity in frontocentral delta and less in frontotemporal, temporoparietal alpha and beta. During sex film subjects showed an increase in delta activity and decreases in temporal alpha and beta activity and parietal alpha. Higher positivity in deceptive than in truthful condition (300–500 ms), higher LPC for deceptive responses to attractive than to unattractive faces (no difference in truthful answers for the LPC), and higher negative slow wave for truthful answers to unattractive than to attractive faces

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Doppelmayr et al. (2003) (abstract)	8 (mean age = 22)	9 (mean age = 25)	Two groups (female and male) perform task with 12 different picture categories (only 2 categories analyzed for results section)	Passive viewing	qEEG	Erotic pictures (erotic females and males)	Event-related synchronization (ERS, frontal and central locations) in the theta band was stronger toward opposite-sex erotic pictures than toward same-sex erotic pictures for both genders. Trend for higher ERS toward pictures of children than toward erotic pictures
Emrich (1978)	4	9 (age missing)	Sample serves as a healthy control group ($N = 13$) which is compared to 2 groups (long viewing times and short viewing times for delinquent pictures) of sexual delinquents when watching 2 different sets of pictures	Passive viewing and rating	ERP (visual inspection)	No sexual stimulation for the healthy control group: pictures of sexual delinquency matched to individual offense of inmates with history of sexual crime	Smaller N2 and larger P3 (frontal sites) for sexual delinquency pictures than for scenery pictures in control group and same pattern for delinquent group with long viewing times but different from delinquent group with short viewing times
Feng et al. (2012)	13	13 (age range [entire sample] = 18–27, mean age [entire sample] = 21.69)	One group performs task with 4 different picture categories displayed within the colored frame	Color (frame) matching task while task irrelevant pictures are displayed within the colored frame	ERP	Erotic pictures (not specified)	P2, N2, P3, and PSW differentiated erotic picture condition from all the other picture category conditions (non-erotic positive, negative, and neutral pictures)
Flaisch et al. (2011)	10	10 (age range [entire sample] = 20–25, mean = 22.4)	One group performs task involving 3 picture categories	Passive viewing (rating after task)	ERP, source localization	Erotic pictures (gestures mediating sexual insult)	Higher EPN (temporooccipital) and LPP (frontocentral) for the sexual insult than for the point and OK gesture. More dipole strength frontocentral, inferior frontotemporal and parietal for the insult than for the OK and the point gesture. The P1 was higher for gestures with emotional content (insult and OK) than for neutral gestures

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Frangos et al. (2005)	9	7 (mean age [entire sample]=23)	One group performs task with 2 different auditory stimuli	Auditory detection during viewing of non-sexual film	ERP (MMN)	Erotic auditory stimulus (sexual suggestive whistle) (manipulated whistle)	Higher MMN (FPz, Fz, FCz, Cz) for sexual suggestive whistle than for other auditory stimuli (manipulated whistle)
Franken et al. (2008)	25	16 (mean age [entire sample]=20.3, SD = 3.1)	One group performs task involving 3 different picture categories	Passive viewing (instructed that questions would follow)	ERP	Erotic pictures (erotic couples)	Erotic pictures showed higher EPN (O1, O2) than neutral or unpleasant stimuli and higher LPP (CPz1, CPz2) than neutral stimuli
Hahn et al. (2016)	13	13 (age range [entire sample]=18–31, mean = 22.1, SD = 2.6)	Two groups (women and men) perform task with 3 different picture categories	Rating task	ERP	Erotic pictures (attractive faces)	No specific ERP results distinguished opposite-sex faces from all other stimuli
Hernández-González et al. (2013)	–	34 (age range = 18–26)	Two groups (each N = 17) perform task	Passive viewing, rating task (right after watching pictures)	qEEG	Erotic pictures (“women wearing sensual clothes (e.g., bikinis) and heterosexual couples engaged in foreplay, oral sex, and sexual intercourse” p. 267)	Erotic group showed decreased interhemispheric correlations in prefrontal beta 1 (F3–F4) and temporal alpha 2 (T3, T4) and also reduced intrahemispheric left prefrontal–parietal (F3–T3) beta 1 correlation and reduced right intrahemispheric prefrontal–parietal (F4, P4) correlation in alpha 2 and theta when compared to the neutral group
Hernández-González et al. (2012)	–	24 (age range = 23–31, mean = 27, SE = 0.044)	Two groups (alcohol and placebo) watch 2 different films	Passive viewing (rating task right after films)	qEEG	Erotic film (scenes from movie “Cat Woman”)	Decreased absolute power in alpha2 (P4) and decreased absolute power in beta1 at P3 for the erotic film. Only within the placebo group did the erotic film elicit higher absolute power in beta2 (F4) than the neutral film

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Hietanen and Nummenmaa (2011): Study 1	–	15 (age range [entire sample]=20–47, mean = 28.27, SD = 8.30)	One group performs task with 4 different picture categories	Identification task	ERP	Erotic pictures (nude bodies)	The erotic film showed lower relative power in alpha2 (F3) and higher delta (F3 and F4). Only within the placebo group did the erotic stimulation show decreased relative power in prefrontal alpha1 (F3 and F4) and increased relative power in beta1 (F4) as well as beta2 (F3 and F4) Erotic film induced lower prefrontal interhemispheric correlation in alpha1, alpha2, beta1 than neutral films. F3-P3 showed higher intrahemispheric correlations in theta band during the erotic film than during the neutral film Erotic pictures elicited higher N170 amplitude than swimsuit bodies or faces. Nude bodies elicited topographies that lasted longer and were more posterior. Naked female bodies elicited also greater N170 than males. N170 latency was further longer for naked bodies than for clothed bodies
Hietanen and Nummenmaa (2011): Study 2	16	16 (age range [entire sample]=19–66, mean = 24.47, SD = 8.32)	One group performs task with 8 different picture categories	Identification task (rating task after main task)	ERP	Erotic pictures (nude bodies)	Erotic pictures elicited higher N170 amplitude for nude bodies than for all other picture categories. The N170 latencies were longer for nude than for clothed bodies. N170 was also higher when the erotic content matched the male subjects preference (nude female bodies > nude male bodies)

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Hietanen et al. (2014)	8	9 (age range [entire sample]=18–30, Mean = 21.9, SD = 3.2)	One group performs 2 tasks with 4 different picture categories	Attention task (rating task after the main task)	ERP	Erotic pictures (nude bodies)	Higher EPN (P7/8, TP7/8, TP9/10), N170 and longer N170 latencies (P7/8, TP7/8, TP9/10) as well as more pronounced LPP (CP1, CP2, CPz, P1, P2, POz, and Pz) in response to erotic pictures when compared to face pictures and clothed bodies
Hou et al. (2016)	20	17 (age range [entire sample]=20–32, mean = 22.8)	One group performs task with 5 different picture categories	Visual discrimination task	ERP	Erotic film (intercourse with heterosexual couple) and erotic pictures (“nude heterosexual couples engaging in intercourse while showing female breasts, but without showing female or male genital areas in close-up” p. 4)	Larger N1, N2, and PSW for sex-related stimulation than for love-related stimulation
Howard et al. (1992)	–	6 (age range = 23–43, mean age = 30.8)	One group performs task with 2 different picture categories	Picture matching task (S1 is compared to S2) and rating with picture of male nudes and with pictures of female nudes	ERP (CNV)	Erotic pictures (female and male nudes)	Higher CNV (Cz) in condition with female nudes than with male nudes

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Howard et al. (1994): Study 1	14 (age range = 20–44, mean = 31.7)	10 (age range = 17–42, mean = 28.4)	Two groups (males and females, comparisons are made to the sample from Howard et al., 1992) perform task with 2 different picture categories	Picture matching task (S1 is compared to S2)	ERP (CNV)	Erotic pictures (female and male nudes)	Higher CNV (C3 and C4) in condition with nudes matching sexual preference than in condition with nudes not matching sexual preference but only in the control group from Howard et al. (1992) was this difference significant. In addition, CNV ($R > L$) asymmetry is reported for homosexual samples but not for heterosexual samples
Howard et al. (1994): Study 2	–	19 (age range = 20–54, mean = 38.1)	Sample serves as a healthy control group ($N = 19$) which is compared to one group of sexual offenders in a task with 6 different picture categories	Picture matching task (S1 is compared to S2), same task as in study 1 but with different sets of picture categories	ERP (CNV)	Pictures of male adults, female adults for the healthy group and male pubescents, female pubescents (both 12–13-year-old with visible secondary sexual characteristics), male children and female children (both 9 years old without visible secondary sexual characteristics) for the sexual offenders	Higher CNV (Cz) in condition with adult pictures than with pictures of children and only in the adult picture condition did a match between picture gender and sexual preference lead to a higher CNV (Cz) for the matching picture gender

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Hyun et al. (2008)	–	36	Two groups (18 patients with premature ejaculation [mean age = 45.0, SD = 9.8] and 18 healthy controls [mean age = 45.6, SD = 9.8]) perform task with 2 different films	Passive viewing	qEEG, source localization	Erotic film (not specified)	No difference in current source density between erotic videos and music videos in healthy controls (only on subject level but not on group level)
							Within the patient group (premature ejaculation), alpha band decreases were observed [right insula (Brodmann area 13), right precentral gyrus (Brodmann area 4), superior parietal lobules of both hemispheres (Brodmann area 7)]
							During the erotic movie, the patient group showed significant decrease in the beta-2 band (right parahippocampal gyrus (Brodmann 37), left middle temporal gyrus (Brodmann 21). Sig. decreases in beta-3 band were found in the left middle temporal gyrus
Inssen et al. (2007): Study 1	11	11 (mean age [entire sample] = 23, SD = 5.9)	One group performs task with 5 different picture categories	Word identification task and passive viewing	ERP, source localization	Erotic pictures (not specified)	Higher P2 and reduced N1 as well as delayed N1 latencies for erotica (and mutilations) than for sports, neutral and attack pictures and shorter LP latencies for erotic pictures (and mutilations) than for neutral words
Jin et al. (2017)	–	19 (age range = 19–27, mean = 22.15, SD = 2.43)	One group performs task with 2 different picture categories	Judgment task (primed by a picture and followed by a decision whether to lend money or not) and feedback	ERP	Erotic pictures (attractive female faces)	Priming stage: attractive faces elicited less pronounced N200 than unattractive face

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Johnston and Oliver-Rodriguez (1997)	–	25 (age range = 18–25)	One group performs task with multiple different facial stimulus configurations	Passive viewing and rating task	ERP	Attractive faces	Feedback stage: only within unattractive faces was there a difference in P3 and feedback-related negativity (FRN) resulting from the positive or negative feedback LPC (Factor 2 extracted with principal component analysis: 550 ms, Pz) was influenced by facial configurations related to perceived attractiveness of the faces Only if face gender matched participants sexual preference did LPC and attractiveness ratings correlate
Johnston and Wang (1991)	31 (age range = 20–35)	–	Three groups (pre-ovulatory, ovulatory, postovulatory phase) perform task with 5 different picture categories	Passive viewing (rating after task)	ERP	Erotic pictures	P3 (Fz, Cz, and Pz, averaged and extracted using principal component analysis) was higher for female models than for babies, male models, dermatological cases or people P3 (Fz, Cz, and Pz, averaged and extracted using principal component analysis) in response to picture of male models were more (and babies, if P3 was calculated using principal component analysis) influenced by ovulatory phase than pictures of babies, ordinary people, dermatological cases and female models

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Johnston et al. (1987)	20	20 (age range [entire sample]=18–35, mean =22.8)	Two groups (10 females, 10 males each) perform tasks with 5 different picture categories	Learning task and counting task (rating prior to tasks)	ERP	Erotic pictures (opposite-sex models)	Main effect of picture category on average P4 (600–680 ms, Pz, Cz, Fz) and P3 (300–380 ms, Pz, Cz, Fz) with largest amplitudes for female model slides compared to babies, people, and dermatological cases
Johnston et al. (1986)	20	20 (age range [entire sample]=18–35)	Two groups (10 females, 10 males each) perform tasks with 5 different picture categories	Learning task and counting task (rating prior to tasks)	ERP	Erotic pictures (opposite-sex models)	Main effect of picture category on extracted (principal component analysis) factors 2 (P4: 540 ms, Pz, Cz, Fz) and 3 (P3: 300 ms, Pz, Cz, Fz) with largest factors for female model slides compared to babies, people, and dermatological cases

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Kam et al. (2007)	21	22 (mean age missing)	Two groups (women and men) perform task with 2 different films	Passive viewing	qEEG, source localization	Erotic film (pornographic video)	Men: more beta 1 (13–18 Hz) activity during erotic clip compared to neutral in parahippocampal gyrus, and left uncus, superior temporal gyrus of both temporal lobes and the middle left occipital gyrus More beta 2 (19–21 Hz) activity in superior frontal gyrus and right medial frontal gyrus and the left anterior cingulate gyrus More beta 3 (22–30 Hz) activity in the middle occipital gyrus, the superior temporal gyrus, the right precuneus, the right superior parietal lobule, the right medial frontal gyrus and superior frontal gyrus, the right anterior cingulate gyrus and the left parahippocampal gyrus Women: more delta (1–3 Hz) activity during erotic clip compared to neutral clip in postcentral gyrus and left inferior parietal lobule and the left middle frontal gyrus More theta (4–7 Hz) activity in the left middle occipital gyrus, the left cuneus and the left postcentral gyrus More alpha (8–12 Hz) activity in the left superior temporal gyrus and the left postcentral gyrus More beta 1 (13–18 Hz) activity increased in the superior temporal gyrus, the left postcentral gyrus, and the left parahippocampal gyrus

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Keil et al. (2003)	13	9 (mean age [entire sample]=26.4)	One group performs task with 6 different picture categories	Passive viewing (rating task after main task)	qEEG, ERP	Erotic pictures (erotic couples)	No specific EEG effects distinguishing erotic pictures from other picture categories (effects reported for pleasant picture category where erotic pictures and family pictures are grouped together and compared to neutral or unpleasant pictures)
Keil et al. (2009)	8	8 (mean age [entire sample]=23.5)	One group performs task with 3 different picture categories	Passive viewing (rating task after main task)	ERP	Erotic pictures (erotic couples)	During viewing of erotic and attack pictures a left-hemispheric intraparietal to inferotemporal connection and a right-hemispheric precuneus to calcarine connection were significantly more frequent than during neutral pictures
Knott et al. (2016)	–	20 (mean age=41.55, SD=2.75)	One group performs task with 4 different picture categories; sample serves as a healthy control group ($N=20$) which is compared to one group of pedophiles	Passive viewing (rating task after main task)	ERP	Erotic pictures	Erotic pictures elicited larger early frontocentral potentials (P2, N4 at Fz) than all the other stimuli and higher LPP (Pz) were found for erotic than for all other pictures
Krug et al. (2000)	11 (age range=21–32)	–	One group performs two tasks during ovulatory phase, the luteal phase, and menses with both tasks involving 4 different picture categories	Affective processing task (rate picture as positive, neutral or negative) and structural processing task (count number of lines)	ERP	Erotic pictures (nude men)	In the affective task, the phase of menstrual cycle influenced the P3 (Fz, Cz, Pz) particularly in response to sexual stimuli and highest P3, LPC (Fz, Cz, Pz) were observed for erotic stimuli during the ovulatory phase. SW was highest to sex stimuli and pictures of body care in the affective processing task, while no effect of cycle was reported for this component

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Kuhr et al. (2013)	–	17 (mean age = 23.88, SD = 4.66)	One group performs task with 4 different pictures	Rating task	ERP	Erotic pictures (nude women)	Enhanced P1, N1, and LPP in response to erotic pictures compared to pictures of sports, dressed women, and daily activities
Kwon et al. (2011)	–	22	Two groups (11 patients with premature ejaculation [mean age = 36.9, SD = 7.8], 11 healthy controls [mean age = 24.2, SD = 1.9]) perform task with 1 film	Passive viewing (rating task after main task)	qEEG, source localization	Erotic films (not specified)	No sertraline effects on EEG reported within the control group In the patient group sertraline increased the high beta frequency in superior frontal gyri (both sides) and in the right medial frontal gyrus When the patient group was compared to the control group, sertraline showed less activity in the beta frequency (middle and superior temporal gyrus as well as fusiform gyrus, lingual gyrus, inferior occipital gyrus, cuneus [right]) in the patient group than in the control group Difference in delta activity for erotic pictures compared to non-erotic pictures
Langevin (2014)	–	16 (age missing)	One group performs task with 4 different picture categories	Passive viewing	qEEG	Erotic pictures (heterosexual intercourse and adult nude females)	Compared to music videos, erotic videos decreased the left-hemispheric high beta frequency band (22–30 Hz) in the middle frontal gyrus, the precentral gyrus, the postcentral gyrus, and the supramarginal gyrus
Lee et al. (2010)	–	11 (mean age = 25.9, SD = 1.22)	One group performs task with 2 different films (once before and once after sertraline)	Passive viewing	qEEG, source localization	Erotic films (not specified)	

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Legrand et al. (2013)	11	11 (age range [entire sample]= 3.7, mean = 26)	Two groups (male and females) perform task with 4 different picture categories under subliminal and supraliminal conditions	Decision task	ERP, source localization	Erotic pictures (computer-generated)	N1 (occipital) was enhanced for naked than for dressed bodies, and this effect was stronger in supraliminal conditions than in subliminal conditions and more pronounced when stimuli were of the opposite sex. Only opposite-sex pictures showed a difference in the subliminal condition between dressed and naked Source localization revealed for supraliminal opposite-sex naked bodies BA17–19 (right calcarine sulcus/lingual gyrus) and BA39 (middle occipital right gyrus) as possible sources and the superior and middle temporal right gyrus. In the subliminal condition, the calcarine fissure and the lingual gyrus bilaterally (BA 17 and 18) as well as the left fusiform gyrus (BA19 and 32) were located
Lifshitz (1966)	–	10 (age range = 18–33)	One group performs task with 3 different picture categories	Passive viewing	ERP (visual inspection)	Erotic pictures (nude females)	Visual inspection suggests different ERP (occipital or occipitoparietal at about 400 ms post-stimulus) for pictures of nude females than for pictures of scenic photographs or ulcerated legs
Lu et al. (2014)	12	12 (mean age [entire sample] = 21.3, SD = 1.5)	Two groups (men and women) perform task with 6 different picture categories	Rating task (and rating task after main task)	ERP	Erotic pictures (attractive cartoon faces)	Higher N170 for attractive than unattractive faces for males (reverse pattern for female participants) Larger LPC for attractive than unattractive faces

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Lübke et al. (2012): Study 1	–	28 (age range = 20–44, mean = 28.5, SD = 7.2)	Two groups (14 homosexuals, 14 heterosexuals) perform task with 3 different odors	Odor rating and detection	ERP, source localization	Erotic smell (axillary sweat from heterosexual women and gay men)	Shorter latency of the P2 component if odor donor matches sexual orientation
Lübke et al. (2012): Study 2	28 (age range [entire sample] = 20–45, SD = 29.5, SD = 7.2)	–	Two groups (14 homosexuals, 14 heterosexuals) perform task with 3 different odors	Odor rating and detection	ERP, source localization	Erotic smell (axillary sweat from heterosexual male and lesbian women)	Shorter latency of the P2 component if odor donor matches preferred gender
Ma et al. (2015)	–	24 (age range [entire sample] = 18–26, mean = 22.19, SD = 1.78)	One group performs task with 2 different picture categories	Ultimatum game	ERP	Erotic pictures (attractive faces)	Face perception: N2 was higher for unattractive faces than attractive faces and LPP was higher for attractive than unattractive faces Feedback stage: Attractiveness influenced the FRN, while the feedback influenced the FRN only in the unattractive face condition
Ma et al. (2017a)	–	38 (age range = 18–26, mean = 21.9, SD = 1.912)	One group performs task with 2 different picture categories	Rating task (and rating task after main task)	ERP	Erotic pictures (attractive faces)	Smaller N2 and larger P300, LPP for attractive faces compared to unattractive faces
Ma et al. (2017b)	18 (age range = 20–25, mean = 22.08, SE = 1.58)	–	One group performs task with 2 different picture categories	Ultimatum game	ERP	Erotic pictures (attractive faces)	Face perception: Attractiveness had an effect on N2 and LPP (similar effects, when the sample from Ma et al. 2015 was included in the analysis) Feedback stage: Attractiveness influenced the FRN while the feedback influenced the FRN only in the unattractive face condition

Table 5 (continued)

Study	Sample	Study design	Task	EEG	Sexual stimulation	Results	
Makarchouk et al. (2011)	Female 18 (age range = 18–21)	Male –	One group performs task during the follicular, ovulatory phase and lutein phase involving 4 picture categories	Passive viewing	qEEG	Erotic pictures (“erotically coloured pictures” p. 363)	Erotic pictures decreased alpha and low-frequency beta in parietal/occipital and right temporal sites. During the ovulatory phase, erotic pictures decreased the low-frequency beta activity in the occipital sites as well as the power of the theta activity in T4. In the lutein phase, such a decrease (during erotic stimulation) in the theta activity was observed in the right temporal sites T4, T6. In poststimulus time period in the ovulatory phase, there was a power increase in the alpha and beta rhythms (posterior sites) and theta activity (right central and temporal) C4, T4. In the lutein phase, there was an increase in beta activity (occipital, mostly right)

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Marzi and Viggiano (2010)	9	8 (age range [entire sample]= 22–30, mean = 26)	One group performs task with 4 different picture categories	Rating task and recognition task	ERP	Erotic pictures (attractive faces)	Rating task (learning): higher early frontal positivity (150–200 ms) for attractive than unattractive faces in frontal sites (interaction with site). Higher N170 for attractive than unattractive faces. Higher EPN for attractive than medium, unattractive or low attractive faces. Higher LPP for highly attractive than unattractive or low attractive faces on centroparietal and parietal sites (interaction with site). Further effect of attractiveness at 500–700 ms
Mastria (2014) (Dissemination): Study 1	18	12 (age missing [entire sample])	One group performs task with 3 different picture categories	Passive viewing, habituation and categorization task	ERP	Erotic pictures (erotic and romantic couples)	Recognition task: Effect of attractiveness on early frontocentral positivity (150–200 ms) only for memorized/previously seen faces. Effect of attractiveness on N170 in T6 (interaction with site)
Mastria (2014) (Dissemination): Study 2	15	11 (age missing [entire sample])	One group performs task with 3 different picture categories	Passive viewing and habituation task	ERP	Erotic pictures (erotic and romantic couples)	Higher LPP (centroparietal) for erotic than for neutral (but not compared to unpleasant) pictures
Mercado et al. (2006)	21	6 (age range [entire sample]= 20–33, mean = 22.07)	Two groups (high trait anxiety, low trait anxiety) perform task with 4 different pictures	Auditory oddball task during passive viewing (rating after main task)	ERP	Erotic pictures (opposite-sex nudes)	Higher LPP (centroparietal) for erotic than for neutral (but not compared to unpleasant) pictures Low-state-anxiety subjects showed higher P2 (deviant auditory stimulus) during erotic pictures than during pictures of a wolf jaw, neutral or a relaxing picture (high-state-anxiety subjects showed higher amplitude to pictures of a wolf jaw)

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Miller (1985) (Dissemination)	33	(male/female ratio not reported)	One group performs task with 5 different picture categories	Learning task (rating prior to task)	ERP	Erotic pictures (opposite-sex models)	Largest P3 (Fz, Pz, Cz) for erotic pictures compared to babies, people, dermatological photographs, further main effect of stimulus category on N2, N3, P4 and extracted (principal component analysis, varimax rotation) factors 4 (320 ms), 5 (200 ms) from the ERP
Minnix et al. (2013)	20	200	Two groups (smokers [N = 180, mean age = 45.1, SD = 10.6] and non-smokers [N = 40, mean age = 46.2, SD = 11.0]) perform task with 10 different picture categories	Passive viewing	ERP	Erotic pictures (erotic couples)	Higher LPP for erotic pictures than for pictures of sad, romantic, neutral pictures and pictures of cigarettes (but erotic pictures were not differentiated from mutilations)
Muñoz and Martín-Loeches (2015)	10	10 (age range [entire sample] = 18–25, mean = 21.7, SD = 2.1)	Two groups (women and men) perform task with 12 different picture categories	Rating task	ERP	Erotic pictures (attractive bodies and faces)	Attractive (beautiful) stimuli elicited a higher P300 than neutral or ugly stimuli (and increased LPC compared to neutral but not ugly stimuli)
Nager et al. (2011)	–	11 (age range = 24–35) and 1 patient (age = 52)	One group and one patient with chronic cluster headache perform task with 4 different picture categories	Passive viewing	ERP	Erotic pictures (“undressed women in explicit poses” p. 331)	Higher amplitude positivity (Pz, Fz, Cz) for the erotic stimuli than for all the other stimuli (dressed bodies, objects, food, car) Intracranial recordings in posterior inferior hypothalamus from the patient showed more enhanced biphasic response (about 200 ms after stimulus) for erotic than all other stimuli

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Oliver (2014) (Dissertation with effect sizes) later published in Oliver et al. (2016)							
Oliver et al. (2016)	19	19 (mean age [entire sample]=26, SD = 5.42)	Two groups (men and women) perform task with 2 different film categories	Auditory oddball task during passive viewing	ERP	Erotic films (“Sweet Lady”)	Trend toward higher NI (probe) amplitudes in erotic compared to neutral films when neutral films were presented first
Ortigue and Bianchini-Demicheli (2008)	4	9 (mean age [entire sample] = 19.1, SD = 1.96)	One group performs task where pictures have to be chosen or rejected	Decision task	ERP, source localization	Erotic pictures (“whole-body models in swimsuits”, p. 339)	142–187 ms after presentation of the pictures a distinct scalp topography (source: right occipitotemporal), more present for high rated pictures, and a distinct scalp topography (source: right occipitotemporal region), more present for low-rated pictures, were detected
Poli et al. (2007)	10	10 (age range [entire sample]=21–30, mean = 24.85, SD = 2.21)	One group performs task with 6 different picture categories	Passive viewing and rating task	ERP (CNV)	Erotic pictures (erotic couples)	Larger SPN (second stage of CNV) for high arousal (including erotic) pictures LPP1 with greater positivity for erotic pictures than the rest (pictures of nature, pollution, household objects or neutral people) and LPP2 with greater positivity for pictures of injuries and erotic pictures
Prause (2007) (Dissertation)	33	33	Three groups (low, medium and high sexual desire) perform task with 4 different picture categories	Rating task and acoustic startle modulation task	qEEG, ERP	Erotic pictures (subcategories of explicit and less explicit content)	Less alpha activity (Pz) for erotic than for pleasant, unpleasant or neutral pictures (all participants) Higher P300 (Pz, POz) and later peak latency (Pz, POz, Oz) for erotic pictures than for non-sexual pleasant, unpleasant or neutral pictures

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Prause et al. (2016)	5	15 (mean age [entire sample]=34.6, SD=10.9)	One group performs task with 2 different incentives and 2 different stimulations (TMS)	Incentive delay task	qEEG	Erotic contact (vibratory incentive in genitalia)	Reduced alpha activity during anticipation and reception of vibratory incentive compared to monetary incentive. Alpha activity differentiated between wins and misses only in the vibratory incentive condition (not in the monetary)
Prause et al. (2014)	22	43 (age mean [entire sample]=24, SD=6.5)	One group performs task with 2 different film categories	Passive viewing and rating task	qEEG	Erotic films (“...consensual, erotic, heterosexual encounter were edited to equal parts kissing/foreplay, oral sex being performed on the man and then the woman, and penile-vaginal intercourse.” p. 228)	Alpha (F3/F4) decrease (both hemispheres) in sexual film compared to neutral film. Decrease was greater in right hemisphere. Further alpha (F7/F8) increase (left) and decrease (right) in the erotic film. Similar results at sites FP1/FP2 Asymmetry scores decreased during sexual film (higher right alpha during neutral film, and decreased difference between right and left alpha during erotic film)
Prause et al. (2015a)	36	86	Two groups (controls [N=67, 23 women, mean age=24, SD=6.5], hypersexual group [N=55, 13 women, mean age=24.4, SD=4.9]) perform task with 4 picture categories	Passive viewing	ERP	Erotic pictures (penetrative sexual behavior with man and woman)	Higher EPN for sexual than neutral or unpleasant pictures. Higher LPP for erotic pictures than pleasant, neutral, and unpleasant pictures and the more explicit erotic pictures resulted in a higher LPP than the less explicit erotic pictures There was a less pronounced LPP in participants with problems related to viewing visual stimuli and in participants with higher sexual desire

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Prause et al. (2015b)	36	86	Two groups (hypersexual [N = 55, 13 females, mean age = 24.4, SD = 4.9] and controls [N = 67, 23 females, mean age = 24, SD = 6.5]) perform task with 4 different picture categories	Passive viewing	ERP	Erotic pictures (penetrative sexual behavior with man and woman)	Highest LPP was recorded for erotic pictures (compared to unpleasant, pleasant non-sexual, and neutral pictures). Lower LPP (C3, Cz, C4, CP3, CPz, CP4, P3, Pz, P4) for hypersexuals compared to controls when watching erotic pictures
Price et al. (2012)	16	15 (age range [entire sample] = 18–24)	One group performs task in 2 different postures and with 2 different picture categories	Passive viewing, startle reaction and rating	ERP	Erotic pictures (“pairs of men and women in sexual situations” p. 213)	Larger P1 (POZ, OZ, O1, and O2) for erotic than for neutral pictures and taking on an approaching posture further increased P1 (POZ, OZ, O1, and O2) and LPP (Cz) for erotic pictures
Proverbio et al. (2010)	20	20 (age range [entire sample] = 20–30, mean = 22.3, SD = 2.7)	Two groups (women and men) perform task with 3 different picture categories	Detection task	ERP, source localization	Erotic pictures (attractive faces)	Shorter N400 latency and larger N400 amplitude for opposite-sex faces than same-sex faces Opposite-sex faces were related to the bilateral limbic areas with left-hemispheric asymmetry (bilateral uncus [BA38], parahippocampal gyri, BA28/35), bilateral fusiform gyri in the temporal lobe (BA37, BA20/21), cingulate cortex (BA24)
Radilová et al. (1983) (abstract); Study 1	–	12 (mean age = 24.3)	One group performs task with 2 different picture categories	Passive viewing	ERP	Erotic pictures	Larger P300 (occipital region) for erotic pictures compared to non-erotic pictures (landscapes, flowers)

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Radilová et al. (1983) (abstract); Study 2	–	6 (age range = 19–29, mean = 23.3)	One group performs task in 2 different emotional states	Passive viewing of erotic pictures till erection and followed by presentation of geometrical figures (number of squares) during erection and without erection	ERP	Erotic pictures	P300 (occipital region) during viewing of geometrical figures was lower during state of erection than without erection
Rellecke et al. (2011)	10	10 (age range [entire sample]=20–32, mean = 25.5)	One group performs task with 3 different picture categories	Auditory discrimination and rating task	ERP	Erotic pictures (attractive faces)	Facial attractiveness had an effect on EPN and LPP
Renner et al. (2012)	28	12 (age range [entire sample]=20–32, mean = 23.4, SD = 3)	One group performs task with 2 different picture categories	Risk evaluation task	ERP	Pictures (opposite-sex persons with estimated risk of sexually transmitted disease)	HIV risk estimates had an effect on early (220–340 ms) potentials in interaction with site. Higher LPP for high-risk persons than low-risk persons while estimated attractiveness had no effect on this component
Ruiz-Díaz et al. (2012)	12	19 (mean age [entire sample]=22.9, SE = 3)	Six groups perform 2 different tasks after watching 3 different films	Passive viewing, rating task (right after watching film) and Tower of Hanoi (HANOI) or Wisconsin Card Sorting Test (WCST) after film	qEEG	Erotic film (scenes from movie “Cat Woman”)	Increased interprefrontal EEG correlation (delta band in F3 and F4) during HANOI after watching erotic video than after watching aggressive or neutral videos and decreased interprefrontal EEG correlation (delta and theta band in F3 and F4) during WCST when watching erotic video than when watching neutral or aggressive video. Within the erotic condition increased delta, theta and alpha were most pronounced during the HANOI task A trend was observed for increased theta activity (interprefrontal) during HANOI task after erotic film

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Schacht et al. (2008)	13	5 (mean = 24.2, SD = 3.54)	One group performs 2 tasks with 3 different picture categories	Gender identification and rating task	ERP, source localization	Erotic pictures (attractive faces)	Attractiveness had an effect on the N170 (first sig. effects at 144–164 ms) more pronounced and earlier in the rating task. Similar effects were found for later components (LPC) Effect of attractiveness on early potentials (P100 and N170) was attributed to sources in the fusiform gyrus and the parahippocampal gyrus
Schmälzle et al. (2011)	19	23 (age range [entire sample] = 20–27, mean = 23.7, SD = 2.3)	One group performs 2 tasks with 2 different picture categories	Recognition task, risk evaluation task	ERP	Pictures (opposite-sex persons with estimated risk of sexually transmitted disease)	Higher early potentials (240–300 ms) when risk had to be explicitly judged compared to the recognition task. In the recognition task, high-risk pictures resulted in more pronounced early potentials compared to low-risk pictures (this difference was less pronounced in the explicit risk judgment task) Similar results were obtained in a later time window (430–530 ms) with high-risk and low-risk pictures differentiated in both tasks (in the explicit task also from 550 to 800 ms)
Schomberg et al. (2016)	–	17 (mean age = 23.88, SD = 19–37)	One group performs task with 4 different picture categories	Rating task	ERP	Erotic pictures (nude women)	No specific ERP results distinguishing erotic pictures from others were reported
Schöne et al. (2016)	–	17 (mean age [entire sample] = 23.9, SD 4.7)	One group performs task with 4 different picture categories	Rating task	qEEG	Erotic pictures (undressing women, not naked)	More frontal alpha asymmetry (reduced relative alpha activity in left hemisphere compared to right) when watching erotic pictures compared to sports and dressed women

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Schupp et al. (2000)	16	16 (age missing [entire sample])	One group performs task with 3 different picture categories	Rating task (evaluation of pictures)	ERP	Erotic pictures (opposite-sex nudes)	LPP more pronounced for erotic pictures than for non-erotic positive and neutral pictures Higher LPP (400–700 ms, 700–1000 ms) for erotic couples than for romance pictures and for sports pictures (opposite-sex erotica were not differentiated from romance pictures but from sport pictures) within the positive valence category Probe P3 were smallest for erotic couples and opposite-sex erotica and also smaller compared to romance pictures
Schupp et al. (2004a)	18	22 (age missing [entire sample])	One group performs task with 12 picture categories	Evaluation of pictures and presentation of acoustic startle stimulus during further passive viewing of picture	ERP	Erotic pictures (erotic couples and opposite-sex erotica)	
Schupp et al. (1996) (abstract)	26	26 (age missing [entire sample])	Two groups (female and male) perform task with 5 different picture categories	Passive viewing (with startle probes)	ERP	Erotic pictures (erotic couples, pictures of romantic courtship and attractive opposite-sex nudes)	Probe P3 reduction while viewing sexual pictures. Larger late positivity during erotic pictures than during neutral, unpleasant (grief or violence) or positive (sports) pictures and the effect was more pronounced in male sample
Schupp et al. (2003a)	12	8 (age missing [entire sample])	One group performs task with 3 different picture categories	Rating task (evaluation of pictures)	ERP	Erotic pictures (erotic couples)	Enhanced EPN (temporooccipital) for erotic pictures than for other pleasant or neutral pictures
Schupp et al. (2003b)	8	7 (age missing [entire sample])	One group performs a combination of tasks with 3 different picture categories	Attentional task and counting task	ERP	Erotic pictures (not specified)	Enhanced EPN (temporooccipital) for erotic pictures than for other pleasant or neutral pictures
Schupp et al. (2004b)	14	2 (age range [entire sample]=19–27, mean=21.2)	One group performs task with 6 picture categories	Rating task (evaluation of pictures)	ERP	Erotic pictures (erotic postures with heterosexual couples)	Higher EPN and for erotic pictures than for images of babies and family scenes, neutral images, unpleasant images and images of threat (similar results in LPP)

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Schupp et al. (2006)	4	4 (age range [entire sample] = 20–34, mean age = 24)	One group performs task with 3 picture categories	Passive viewing	ERP, source localization	Erotic pictures (erotic couples)	Higher EPN for erotic than for mutilation and neutral pictures
Schupp et al. (2007)	8	8 (age range [entire sample] = 19–32, mean age = 25)	One group performs task with 3 picture categories	Passive viewing or counting task	ERP, source localization	Erotic pictures (heterosexual couples or single males or females in erotic postures)	Higher EPN and P3 for erotic pictures than for mutilations and neutral pictures
Simons (1982)	13	13 (age range [entire sample] = 18–31, mean = 20)	Two groups (anhedonic 14 [8 male] and control group 12 [5 male]) perform task with 2 different sets of pictures	Passive viewing and reaction time task (S1 to S2)	ERP (CNV)	Erotic pictures (nude females and males)	Larger P3 amplitude (Cz) with tones predicting erotic pictures than tones predicting household objects in the control group
Simons et al. (1979): Study 1	–	24 (age missing)	Two groups (response and no-response group) perform task with 2 different picture categories	Passive viewing and reaction time task (reaction time to S1 influences S2 duration)	ERP (CNV)	Erotic pictures (nude females)	Higher CNV (Cz) to tone signaling erotic pictures than to tone signaling household objects when response was required
Simons et al. (1979): Study 2	–	12 (age missing)	One group performs task with 2 different picture categories	Passive viewing and reaction time task	ERP (CNV)	Erotic pictures (nude females)	Higher CNV (Cz) to tone signaling erotic pictures than to tone signaling household objects
Simons et al. (1979): Study 3	–	12 (age missing)	One group (no-response group only) performs task with 2 different picture categories	Passive viewing and reaction time task (shorter S2 duration than in study 1)	ERP (CNV)	Erotic pictures (nude females)	Higher CNV (Cz) to tone signaling erotic pictures than to tone signaling household objects
Sun et al. (2015)	10	10 (mean age [entire sample] = 23.9, SD = 7.5)	One group performs task with 4 different picture categories	Categorization task	ERP, source localization	Erotic pictures (attractive unmarried faces)	Effect of attractiveness levels was significant left occipitotemporal (220–260 ms) (unattractive faces had a more negative amplitude than attractive faces) There was also an effect in the medial centroparietal area (510–610 ms) and the right temporal region (825–900 ms) and bilateral occipitotemporal (150–200 ms)

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Tagai et al. (2017): Study 1	23 (age range = 20–33, mean = 29.0, SD = 7)	–	One group performs task with 3 different picture categories	Recognition task	ERP	Erotic pictures (attractive female faces)	Different amounts of makeup (rated differently in attractiveness) had an effect on P1 and N170
Tagai et al. (2017): Study 2	22 (age range = 27–35, mean = 32.6, SD = 2.4)	–	One group performs task with 3 different picture categories	Recognition task	ERP	Erotic pictures (attractive female faces)	Different amounts of makeup (rated differently in attractiveness) had an effect on N170 depending on the site
Tamm et al. (2014)	42	20 (age range [entire sample] = 19–51)	One group performs task with 3 different picture categories	Time production task	ERP	Erotic pictures (erotic couples and opposite-sex nudes)	Higher P1 (O1, O2, PO3, PO4) and LPP (Cz, CP1, CP2, Pz) for erotic compared to neutral (but not to negative) pictures and higher EPN (O1, O2, PO3, PO4) for erotic than for neutral and negative pictures
Thiruchselvam et al. (2016)	11	11 (age range [entire sample] = 18–21, mean = 19.63, SD = 0.84)	One group performs task with 2 different picture categories	Rating task	ERP	Erotic pictures (attractive opposite-sex faces)	Attractive faces elicited more pronounced EPN/N200 and LPP than unattractive faces
Trujillo et al. (2014)	30	18 (age mean [entire sample] = 18.60, SD = 0.17)	One group performs task with 3 different picture categories	Categorization task (rating task after main task)	ERP	Erotic pictures	No specific effects on N170 distinguishing high attractive female faces from both low attractive female faces and average attractive female faces; however, such effects are reported for P2 (supplement material)
Tucker and Dawson (1984)	5	4 (age missing [entire sample])	One group performs task involving 2 emotional states	Mood induction through emotional acting	qEEG	Acting sexually aroused with heavy breathing and vasodilation	More right-hemispheric activity (less alpha power) during sexual arousal acting than during depression acting. Higher right coherence in central (intra- and interhemispheric) and parietal theta and parietal and occipital beta 2 (intra-hemispheric) during sexual arousal compared to depression

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Uusberg et al. (2013a)	43	30 (age range [entire sample]=18–29, mean =20.6, SD =1.96)	One group performs task with 5 different picture categories	Rating task (affective) and luminance evaluation/object numerosity task (non-affective)	qEEG	Erotic pictures (heterosexual couples depicted in erotic ways)	Late central upper alpha band (11–15 Hz, FCI/2 and CP1/2) in response to erotic pictures shows pattern distinctive of aversive, unpleasant, pleasant, and neutral pictures
Uusberg et al. (2013b)	46	33 (age range [entire sample]=18–29, mean =20.7, SD =2)	One group performs task with 5 different picture categories	Rating task (affective) and luminance evaluation/object numerosity task (non-affective)	ERP	Erotic pictures (not specified)	Highest EPN (O1, Oz, O2), P3 (CP1, CP2, P3, P4, Pz) and SW (CP1, CP2, P3, P4, Pz) scores for erotic pictures compared to aversive (SW was the same for erotic and aversive pictures), unpleasant, neutral, or pleasant pictures
Uusberg et al. (2014)	32	28 (age range [entire sample]=18–29, mean =20.7, SD =2.1)	One group performs 2 tasks with 5 different picture categories	Rating task	ERP, qEEG	Erotic pictures (opposite-sex couples)	Higher LPP (Pz, PO3/PO4, P3/P4, CP1/CP2) for erotic pictures than for neutral, pleasant, or unpleasant images, but no effect on frontal alpha asymmetry
van Hooff et al. (2011)	20 (mean age =22.4, SD =3.0)	20 (mean age =22.6, SD =3.4)	Two groups (females and males) perform task with 3 picture categories	Orienting task (rating task after main task)	ERP	Erotic pictures (computer-generated opposite-sex attractive faces)	Higher P2 for attractive than for neutral faces (not different to unattractive faces). Males showed higher PSW for attractive faces than for unattractive or neutral faces

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
van Lankveld and Smulders (2008)	–	16 (age range = 19–59, mean = 33.8, SD = 15.1)	One group performs task involving 5 picture categories	Rating task	ERP	Erotic pictures (“nude female individuals and nude heterosexual couples, engaging in female- and male-directed oral sex, and vaginal intercourse, while showing female breasts, but without showing female or male genital areas in close-up.” P. 202)	Erotic pictures elicited higher P3 and PSW (Cz) than any other category (area measures). Only the effect on the P3 was still sig. after ERP’s were rating-corrected
Vardi et al. (2009)	52	–	Three groups (22 patients with sexual dysfunction [9 with Hypoactive Sexual Desire Disorder] [patient age range = 22–61, mean = 33.2, SD = 12.1] and 30 healthy controls [age range = 23–66, mean = 31.4, SD = 11.1]) perform task with 2 different films	Auditory detection task during viewing of erotic film	ERP	Erotic film (either containing or not containing scenes of intercourse)	No difference in P300 (probe) during erotic (intercourse) and non-erotic (no intercourse) film in the healthy group P300 amplitude reduction in intercourse-excluding videos was greater in the patient group
Vardi et al. (2006)	16	14 (age range [entire sample] = 18–45, mean = 29)	One group performs task while film clips of 3 categories are played	Auditory oddball task during passive viewing of videos	ERP	Erotic film (sexually explicit clip)	Larger P300 (Cz) decrease during sexual clip than during sport clips and clips of scenery

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Wacker et al. (2013)	–	181 (age range = 20–35, mean = 23.9, SD = 3.0)	Two groups (placebo and D2 blocker) perform task	Rating task	qEEG	Erotic presence (female experimenter)	Only for the highly attractive rated female experimenters did trait approach motivation scores correlate with frontal alpha asymmetry (this association was reversed with D2 blocker)
Waismann et al. (2003)	–	34 (mean age [entire sample] = 28.8)	One group performs task with 3 different picture categories. This sample serves as a healthy control group ($N = 34$) which is compared to one group of paraphiles	Rating task	ERP (CNV)	Erotic pictures (explicit heterosexual intercourse, oral sex, and female genitalia) and also paraphilic pictures for the paraphiles (“depicting fetishistic and sadomasochistic equipment and activities (themes such as punishment, bondage, humiliation, torture apparatus, transvestism, rubber, leather, and stiletto shoes)” p. 138)	The heterosexual male control group showed higher P600 (P4) to heterosexual pictures than a group of paraphiles
Wangelin et al. (2012)	30	30	Two groups (high and low anxiety) perform task with 6 different picture categories	Passive viewing with acoustic startle task	ERP	Erotic pictures (erotic couples)	Erotic pictures elicited higher LPP and reduced P3 (in response to startle) than emotional faces or neutral pictures (but not violent scenes)

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Wegesin (1998)	40 (20 heterosexuals: mean age = 24.5, SD = 5.4, 20 homosexuals: mean age = 32.6, SD = 7.1)	40 (20 heterosexuals: mean age = 32.2, SD = 4.9, 20 homosexuals: mean age = 25.6, SD = 6.4)	Four groups (heterosexual males, homosexual males, heterosexual females, homosexual females) perform 2 tasks	Mental rotation and lexical-decision/semantic monitoring task	ERP	–	Mental rotation: heterosexual males showed higher slow wave (SW, Pz, P3, P4, T5, T6) than homosexual males and heterosexual females and no group effects in the lexical-decision/semantic monitoring task Higher LPC for attractive than non-attractive faces
Werheid et al. (2007)	11	7 (mean age [entire sample] = 25.5, SD = 5.7)	One group performs task with 2 different picture categories	Rating task (additional rating after main task with a 7-point instead of a 2-point scale)	ERP	Erotic pictures (attractive faces)	Erotic pictures (attractive faces) Higher LPC for attractive than non-attractive faces
Wiedemann et al. (1999)	9	39	Two groups (patients with panic disorder [$N = 23$, mean age = 37.5, SD = 12.40] and control group [$N = 25$, mean age = 35.6, SD = 9.40]) perform task with 4 different picture categories	Rating task and motor task (no pictures)	qEEG	Erotic pictures (not specified)	Lower alpha power in right than left frontal electrode during spider picture than erotic picture in the patient group (no such alpha asymmetry present in the control group)
Wiese et al. (2014)	10	10 (mean age [entire sample] = 24, SD = 2.4)	One group performs 2 tasks with 2 different picture categories	Gender identification and recognition task	ERP	Erotic pictures (attractive faces)	Learning phase: Larger EPN and LPP for attractive faces than for unattractive faces During test: Larger EPN, N170, LPP and smaller P2 for attractive faces than for unattractive faces
Williams and Therman (2011)	16	7	One group performs one task with 4 different association pairs	Gay-straight implicit association test	ERP	Pictures (same-sex couples and opposite-sex couples)	Smaller N400 (Cz, CPz, Pz, FCz) and higher LPP (Pz) for compatible associations compared to incompatible associations
Yang et al. (2008)	15	15 (age range [entire sample] = 20–25, mean = 21.4)	Two groups (male and females) perform task with 4 different picture categories	Evaluation task (appropriate or not)	ERP	Erotic pictures (couple hugging and kissing)	Larger P2 and LPC for pictures with hugging and kissing than for neutral pictures (couples not hugging or kissing)

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Zeng et al. (2012)	–	18 (age range = 19–23, mean = 21.1)	One group performs task with 2 different picture categories	Decision task	ERP	Erotic pictures (sexy female)	Higher N2 and LPC during decision stage in task S (involving sexy female) than in task B (involving beautiful female) and higher LPC when a sexy female was chosen over money in task S
Zhang et al. (2011)	7	7 (age range [entire sample] = 18–24, mean = 21.67)	One group performs 2 tasks with 2 different picture categories	Rating (judgment) and recognition task	ERP	Erotic pictures (attractive faces)	Rating (judgment) task: higher N300 (frontocentral sites) and LPC (central sites) for attractive than unattractive faces Recognition task: higher P160, LNP (frontocentral), LPC (central) more pronounced for attractive faces than for unattractive faces
Zhang et al. (2010)	–	13 (age range = 19–25, mean = 22.35)	One group performs 2 tasks with 2 different picture categories	Rating (judgment) and recognition task	ERP	Erotic pictures (attractive faces)	Rating (judgment) task: higher N300 and P350 (prefrontal, frontal and central sites) for attractive than unattractive faces Recognition task: higher P160, N300 (prefrontal, frontal and central sites), P500 (LPC, parietal and central) in response to attractive than to unattractive faces
Zhang et al. (2012)	8	8 (age range [entire sample] = 18–24, mean = 21)	One group performs task with 2 different picture categories	Rating task (and rating task after main task)	ERP	Erotic pictures (attractive faces)	More positive P2 (150–220 ms) for attractive than unattractive faces. More negative (300–380 ms) amplitudes for unattractive than for attractive faces. More positive response (380–500 ms) for attractive than unattractive faces (PCA: 200–300 ms, and 250–800 ms factors showed more positive responses to attractive than to unattractive faces)

Table 5 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Zhang et al. (2014) with data from Zhang et al. (2012)	–	–	–	–	Source localization	–	Dipole source of the P300 was localized in inferior and superior frontal gyrus as well as angular gyrus, supramarginal gyrus, inferior and superior temporal gyrus, and occipital gyrus and lingual gyrus
Zhang et al. (2016a)	17	17 (age range [entire sample] = 18–24, mean = 21.63, SD = 1.51)	Two groups (female and male) perform task with 2 different picture categories	Location matching task and recognition task	ERP	Erotic pictures (attractive faces)	Larger P1 for attractive than unattractive faces in male sample Larger N170 for attractive faces that were seen before in male sample Larger P2 for attractive faces that were seen before in male sample compared to female sample
Zhang et al. (2016b)	8	8 (age range [entire sample] = 19–24, mean = 21.30, SD = 1.92)	One group performs task with 2 different picture categories and 2 priming conditions	Priming task with color identification	ERP	Erotic pictures (attractive faces)	Attractive faces elicited larger P2 (FC3, FC4, FCz) than unattractive faces and larger 350–550 ms amplitude in frontal (F3, F4, Fz), frontal-central (FC3, FC4, FCz), and central sites (C3, C4, Cz). Congruent priming trials (irrespective of attractiveness) elicited also smaller N2 compared to incongruent trials
Zhen et al. (2011)	55 (age range = 23–30, mean = 26, SD = 2)	–	One group performs task with 2 different categories of music	Auditory oddball task during relaxing music or sexual auditory material and (rating after main task)	ERP	Erotic auditory stimulus (sexual music: Mea Culpa, Principles of lust, and the rivers of belief)	Lower P3 amplitude (probe) during sexual music compared to relaxing

more appealing, it influenced the LPC and beauty ratings but only in response to the opposite-sex faces and not the same-sex faces (Johnston & Oliver-Rodriguez, 1997). Based on the theory of sexual selection, it was assumed that characteristics could be attractive to the opposite sex because they suggest enhanced reproductive success (Johnston & Oliver-Rodriguez, 1997). The CNV studies replicated the preference-dependent effects only for heterosexual males but not for homosexual males or females (Howard et al., 1992, 1994). In a second study involving the heterosexual sample only, the preference-dependent effects were not only shown based on the gender of the target picture but also by virtue of the age of the female on the picture, with adult females eliciting higher CNV than child females (and pubescent females taking an intermediate place). Similarly, diminished effects were also shown with paraphilic picture content (Waismann, Fenwick, Wilson, Hewett, & Lumsden, 2003). While amplitude or latency measures did not differentiate between the heterosexual and both homosexual groups in the first study, some differences were found in hemispheric asymmetries within the CNV (Howard et al., 1994). Hemispheric asymmetries in relation to erection and orgasm, as mentioned above, were not replicated consistently, although not many studies recorded EEG during such states following the study by Rosen et al. (1986). The concept of asymmetry was picked up, however, in studies looking at sexual arousal without any focus on penile tumescence or orgasm.

Tucker and Dawson (1984) asked method actors to act out different emotional states including sexual arousal and a depressive state. Right-hemispheric activity was higher (less alpha power) during sexual aroused acting than during depressed acting. Again, the right-hemispheric importance for sexual arousal was emphasized. Later studies used cognitive tasks, in which either gender differences in performance was assumed or cognitive tasks that were supposed to target only the left or the right hemisphere (e.g., mental arithmetic task to target only the left hemisphere; e.g., Kirenskaya-Berus & Tkachenko, 2003). With such settings, including EEG recordings during resting state, these studies tried to differentiate sexual preferences without the use of any sexual stimulation. This procedure implies that different contents according to sexual preference would be represented in structural brain differences that can also be differentiated with neuroelectric signals during rest or during performance activation without any sexual context. This implication was pursued more thoroughly within the research on abnormal sexual preferences (see below). Still, some studies were conceptualized to distinguish between hetero- and homosexual orientation. Alexander and Sufka (1993) used verbal and spatial tasks on male homo- and heterosexuals and female heterosexuals. No group differences were found in performance as measured with behavioral data. Asymmetries in alpha during resting state differentiated the homosexual male group from the two

heterosexual groups and only from the male heterosexuals in the verbal task. All tasks also involved an emotional framing since each trial asked for affective judgment (in one task on facial stimuli) and the resting state measurement comprised multiple resting segments spread within the affective trials at the beginning of each block instead of one long recording during rest in isolation. Neuroelectric group differences could therefore be a result of different affective influence between the groups that might have carried over from the affective processes to the cognitive tasks. In a similar experimental setting without any demands on affective processing heterosexual males showed higher slow waves (1800–3700 ms) than homosexual males or heterosexual females during a mental rotation task—a pattern that was also reflected in the performance measures based on behavioral data (Wegesin, 1998). These studies (Alexander & Sufka, 1993; Wegesin, 1998) were conducted within the framework of psychosexual differentiation, i.e., behavioral and neurophysiological properties develop differently between the sexes and also between heterosexuals and homosexuals within the same gender (Meyer-Bahlburg, 1993).

Later studies departed from cognitive performance measures and focused on picture categories with different emotional contents again, with the advent of the first studies looking at frequency bands and current source densities during erotic picture stimulation (Doppelmayr, Stadler, Sauseng, Rachbauer, & Klimesch, 2003) and erotic films (Dimpfel, Wedekind, & Keplinger, 2003) as well as first ERP studies on erotic auditory stimuli (Frangos, Ritter, & Friedman, 2005). Event-related synchronization in theta was higher for erotic pictures matching preference than for non-matching ones (Doppelmayr et al., 2003). In addition, erotic and sexually explicit film clips were associated with differences in band frequencies within multiple cortical areas (Dimpfel et al., 2003) although this was observed in comparison with a neutral resting stage only, not in response to other emotional stimuli. Also, the film category labeled as erotic is only mentioned to show female and not male content. Within the auditory modality, sexually suggestive whistles elicited higher MMN than distorted whistles (Frangos et al., 2005). If the semantic content of non-linguistic stimuli was sexual, it influenced the MMN even if no such effects were observed with the behavioral data.

Substantial work was done in the field of ERPs and emotional images (Schupp, Junghöfer, Weike, & Hamm, 2003a, b; Schupp et al., 2000, 2004a, b, 2006, 2007). These studies made effort in choosing a variety of different picture categories from the International Affective Picture System (Lang, Bradley, & Cuthbert, 1999). Pictures were usually chosen based on ratings in dimensions of emotional valence and emotional arousal and could be rated again by the participating sample to ensure that the pictures used actually evoked the emotions intended. This allowed for conducting studies

with controlled yet differential visual emotional effects on ERPs. In these experiments of erotic stimuli elicited higher EPN, P3, and LPP compared to a variety of neutral pictures, other pleasant ones, and unpleasant pictures in multiple tasks requiring visual attention. Moreover, the specificity of the response toward erotic stimuli turned out to be robust against habituation effects in repeated trials (Schupp et al., 2006, but for similar habituation effects on pictures of sexual insult and neutral pictures see Flaisch, Häcker, Renner, & Schupp, 2011). The effects of erotic stimuli were also present when the task did not require emotional processes and the emotional picture content was irrelevant for task success (Schupp et al., 2003a). Similar effects were further reported when the P3 in response to a startle probe during erotic picture viewing was analyzed (Schupp et al., 2004a). Sometimes erotic pictures were differentiated from all other picture categories (e.g., Schupp et al., 2004b, 2006, 2007). In some instances, pictures of mutilated bodies (usually rated with unpleasant valence and as highly arousing) were the only ones not differentiated from erotic pictures (usually also rated as highly arousing but with pleasant valence) (e.g., Schupp et al., 2000, 2003b). Most pronounced potentials for erotic pictures and pictures of mutilations or human attacks with no difference between these two most extreme categories were also reported in later studies (De Cesarei & Codispoti, 2011; Ihssen, Heim, & Keil, 2007; Keil et al., 2009; MASTRIA, 2014; Uusberg et al., 2014). Early ERP components might differentiate better erotic pictures from mutilations than later ERP components (e.g., De Cesarei & Codispoti, 2006). Comparable effects of erotic pictures and mutilations (both compared to neutral pictures) were still present after 60 repetitions, hinting toward a similar resilience for habituation effects between the two categories (Codispoti, Ferrari, & Bradley, 2006, 2007) with a somewhat superior resistance for erotic pictures in occipitotemporal and centrofrontal sites (Codispoti et al., 2007). The reported effects of erotic visual stimuli on EEG so far seemed to be driven by emotional intensity as measured by arousal ratings. In one study though, erotic pictures were rated more highly than sports images in terms of arousal exclusively yet the ERPs (area measures for P3 and positive slow wave, PSW) toward erotic pictures were far more pronounced than would have been expected from an additive effect of valence and arousal ratings (van Lankveld & Smulders, 2008). In other studies, similar arousal and valence ratings were measured for erotic and non-erotic positive images, yet those picture categories were differentiated in P2, N2, P3, PSW (Feng et al., 2012) as well as in N1 and P1 (Kühr, Schomberg, Gruber, & Quirin, 2013). Analogous effects were replicated for LPP (Uusberg et al., 2014), EPN, P3 (Uusberg et al., 2013b) and alpha activity even when differences in physical properties between the picture categories were taken into account (Schöne, Schomberg, Gruber, & Quirin, 2016; Uusberg,

Uibo, Kreegipuu, & Allik, 2013a). Alpha asymmetry again seemed to play an important role in processing erotic content (e.g., Prause, Staley, & Roberts, 2014). These findings were consistent with the hypothesis that the emotional and motivational significance of a stimulus could be inferred from EEG signals. It was assumed that less voluntary and more reflexive attentional processes are prompted by the emotional significance of a stimulus in terms of survival or reproductive success (e.g., Schupp et al. 2003a, b, 2004a, b). Within this theory, EEG response seemed most pronounced when contents of sex and violence were encountered.

There was a great rise in the number of studies focusing on ERPs and using erotic pictures in recent years. More studies replicated the effects on the P3 and later components (Bartholow, Lust, & Tragesser, 2010; Briggs & Martin, 2008, 2009; Franken, Muris, Nijs, & van Strien, 2008; Hietanen, Kirjavainen, & Nummenmaa, 2014; Knott, Impey, Fisher, Delpero, & Fedoroff, 2016; Minnix et al., 2013; Tamm et al., 2014) with similar results for erotic films (Vardi et al., 2006) and attractive faces (Dong, Wu, & Lu, 2010; Wangelin, Bradley, Kastner, & Lang, 2012; Werheid, Schacht, & Sommer, 2007; Zhang, Zheng, & Wang, 2016b). Effects on earlier components were also replicated (Alho, Salminen, Sams, Hietanen, & Nummenmaa, 2015; Bailey, West, & Mullaney, 2012; Briggs & Martin, 2008; Franken, Muris, Nijs, & van Strien, 2008; Hietanen et al., 2014; Hietanen & Nummenmaa, 2011; Knott, Impey, Fisher, Delpero, & Fedoroff, 2016; Mercado, Carretié, Tapia, & Gómez-Jarabo, 2006; Tamm et al., 2014) again with similar results for attractive faces (Rellecke, Bakirtas, Sommer, & Schacht, 2011; Schacht, Werheid, & Sommer, 2008; Zhang et al., 2011, 2016b). A match between sexual orientation and erotic content mediated EEG effects also when pictures of faces were used (e.g., Proverbio, Riva, Martin, & Zani, 2010). Comparable results for erotic stimuli when using PCA or amplitude averages were also replicated (Zhang, Tang, & Zhou, 2012; for source reconstruction, see Zhang, Tang, & Zhou, 2014). Similar effects for erotic stimuli were also found with intracranial recordings (Nager et al., 2011). Studies with a focus on cognitive performance measure (e.g., Tower of Hanoi task) were rare (Amezcu-Gutiérrez et al., 2016; Ruiz-Díaz, Hernández-González, Guevara, Amezcu, & Ágmo, 2012), but the effects of erotic films on qEEG were also replicated (e.g., Hernández-González, Gutiérrez, Martín, Sánchez, & Guevara, 2013; Lee, Hyun, & Kwon, 2010; Ruiz-Díaz et al., 2012). Apart from replications, other studies looked at new forms of stimulation. Brain waves toward erotic stimuli were influenced through pharmacological means (Kwon, Kam, Choi, Do, & Hyun, 2011; Lee et al., 2010; Wacker, Mueller, Pizzagalli, Hennig, & Stemmler, 2013). The effect on early components was increased by taking on an approaching posture (Price, Dieckman, & Harmon-Jones, 2012) and attractive faces affected

late components even when they were computer-animated (Sun, Chan, Fan, Wu, & Lee, 2015; van Hooff, Crawford, & van Vugt, 2011; for animated bodies, see, for example, Del Zotto & Pegna, 2017) or cartoons (Lu, Wang, Wang, Wang, & Qin, 2014). Attractive faces also influenced ERPs to subsequently presented stimuli (Ma, Zhang, Pei, & Abdeljelil, 2017a), while expectancy prior to the face stimuli influenced ERPs elicited by attractive faces (Thiruchselvam, Harper, & Homer, 2016). Subsequently attributed fair or unfair behavior to attractive faces had no influence on ERPs, while there was a distinction when faces were unattractive (Ma, Hu, Jiang, & Meng, 2015; Ma, Zhang, Pei, & Abdeljelil, 2017b; for similar effects on reliability of behavior, see Jin, Fan, Dai, & Ma, 2017). When directly compared, bodies seemed to have a stronger effect on ERPs than faces (Muñoz & Martín-Loeches, 2015). Not only did sexual whistles affect the MMN, as already mentioned (Frangos et al., 2005), but a sexual song (from popular music, recommended by specialists and researchers in music and sex therapy) was shown to influence the P3 (Zhen, Hu, Tao, & He, 2011). The assumed risk for a sexually transmitted disease also influenced ERPs (Renner, Schmälzle, & Schupp, 2012; Schmälzle, Schupp, Barth, & Renner, 2011). Furthermore, the P2 latency was shorter when smelled axillary sweat came from a subject matching ones sexual preference (Lübke, Hoenen, & Pause, 2012). The LPP and N400 were further sensitive to gay-straight associations of words and pictures within the Implicit Association Test (Williams & Themanon, 2011). Apart from pictures, tones, and smells, the alpha activity was influenced by anticipation and reception of genital vibratory stimulation (Prause et al., 2016) as well as from the attractiveness of a female experimenter (Wacker et al., 2013). Early and late components were similarly influenced when the pictures only displayed hugging and kissing (Yang, Ding, Chen, & Zhang, 2008) or gestures of sexual insult (Flaisch et al., 2011). The effect of erotic pictures was also differentiated from pictures displaying themes of romantic love without sexual content (Hou et al., 2016). Effects on N1 were even found when erotic pictures were presented subliminally yet only if the gender of the persons shown matched the sexual orientation of the participants (Legrand, Del Zotto, Tyrand, & Pegna, 2013). Additional effects of erotic pictures were also seen when erotic pictures (Ortigue & Bianchi-Demicheli, 2008; Zeng, Wang, & Zhang, 2012) or pictures of attractive faces were imbedded in decision, orienting, and recognition tasks (Marzi & Viggiano, 2010; Tagai, Shimakura, Isobe, & Nittono, 2017; van Hooff et al., 2011; Wiese, Altmann, & Schweinberger, 2014; Zhang et al., 2010, 2011). Similar effects were shown in priming tasks (Zhang et al., 2016b, location matching task in Zhang, Wei, Zhao, Zheng, & Zhang, 2016a) and a modified trust game (Chen et al., 2012). In one study, participants were asked to fake their attractiveness ratings toward facial stimuli; the ERP captured differences between truthful and

faked responses in response to attractive and unattractive faces (Dong et al., 2010).

Taken together, these studies showed how neuroelectric correlates combined with sexual stimuli were in support of a model of motivated attention and emotional states over the negativity bias since erotic pictures elicited higher ERP than all other picture categories, including mutilations (e.g., Briggs & Martin, 2009). Different adult attachment styles based on attachment theory (Bowlby, 1969, 1982) also seemed to influence ERP toward erotic pictures (Hou et al., 2016). Effects of sexual content influenced ERP not only through emotional but also semantic properties (Williams & Themanon, 2011) and also using different modalities. Erotic stimuli further affected EEG signals during decision processes, supporting the notion from evolutionary-based theories (e.g., Bradley et al., 2003) that a stimulus relevant for reproduction can influence attention and decision (Zeng et al., 2012). In this regard, EEG evidence on the judgment of sexual risk further supported a risk-as-feelings hypothesis (Loewenstein, Weber, Hsee, & Welch, 2001) over a more calculated view of risk assessment (Renner et al., 2012). Similarly, ERP during an ultimatum game was more in support of theory of “beauty premium” (attractive individuals being treated more favorably in the labor market; Hamermesh & Biddle, 1993) than classic economic theory on rational- and self-interest-driven individuals (Ma et al., 2015). Throughout many explanations of the results, visual attention was repeatedly theorized to be an initial and pivotal step in the processing of sexually interesting stimuli.

Other studies were also more interested in participant characteristics than stimulus properties. Besides the mentioned different preferences, sexual desire (Prause, 2007) as well as hypersexuality (Prause, Steele, Staley, & Sabatinelli, 2015a; Prause, Steele, Staley, Sabatinelli, & Hajcak, 2015b), hyposexuality (Vardi et al., 2009), and premature ejaculation (Hyun, Kam, & Kwon, 2008) had an effect on EEG. Other participant characteristics that showed effects on EEG during erotic stimulation were alcohol intake (Hernández-González, Sanz-Martin, Guevara, Amezcua-Gutiérrez & Diaz, 2012), gender (e.g., Demidova, Dubovik, Kravchenko, & Makarchouk, 2014; Kam, Kwon, & Hyun, 2007), panic disorder (Wiedemann et al., 1999), anxiety (Mercado et al., 2006), and anhedonia (Simons, 1982). Erotic pictures also showed higher LPP when compared to cigarette-related pictures in smokers (Deweese, Robinson, Cinciripini, & Versace, 2016; Minnix et al., 2013).

Some studies focused on female subjects exclusively and were intended to find out whether the menstruation cycle could affect ERPs toward erotic pictures (Johnston & Wang, 1991; Krug, Plihal, Fehm, & Born, 2000). Krug et al. replicated the earlier results of Johnston and Wang and found strongest reactions toward erotic stimuli during the ovulation phase. While Johnston and Wang used a counting method

to assess progesterone levels, Krug et al. used actual blood levels to determine menstrual phase and also asked for affective processing of the pictures. The results showed higher P3 and LPC for erotic pictures. The effect of the menstrual cycle on EEG was largest, when pictures involved erotic material (Makarchouk, Maksimovich, Kravchenko, & Kryzhanovskii, 2011). With a large female sample ($N=264$) and the effect of menstrual cycle averaged out, the processing of erotic pictures could be differentiated from the processing of non-erotic images in P2, N4, and the LPP (Anokhin et al., 2006).

Compared with the findings presented above, there are far less published accounts of studies that reported null effects of erotic stimulation on the EEG. This disparity could be due to publication bias toward positive results, at least in part. Other reasons can be found in the specific designs of each study. One study did not differentiate erotic from non-erotic pictures when the pictures were presented in a flickering rate (10 Hz) (Keil et al., 2003). Although when erotic pictures were grouped together with family pictures to create a pleasant stimulation, effects on EEG measures are reported. No different current source densities were found when watching an erotic movie compared to a music clip (Hyun et al., 2008). However, Hyun et al. did report differences on subject level and also differences when this group was compared to a group of patients with premature ejaculation during the erotic movie. Similarly, Vardi et al. (2009) found no differences between erotic and non-erotic clips in the P300. In the study by Vardi et al. (2009) however, the non-erotic clips were still sexual but without showing intercourse and differences in the P300 were observed when this group was compared to a group with sexual dysfunction. It should be noted that ERPs to auditory probes during films seemed less suitable to differentiate between erotic and other film categories in other studies as well (Carvalho, Leite, Galdo-Álvarez, & Gonçalves, 2011; Oliver, 2014; Oliver, Meana, & Synder, 2016). Nonsignificant results were rarely reported when ERPs were measured in response to direct viewing of erotic pictures (Carretié et al., 1997). In Carretié et al., the erotic pictures were shown simultaneously with other pictures next to them that demanded attention in a distracting way as part of the task. In another instance (Kwon et al., 2011), effects of sertraline on EEG measures during an erotic film were only reported in comparison with a patient group but not within the healthy control group. Other studies showed no effect of attractive faces (Hahn et al., 2016; Trujillo, Jankowitsch, & Langlois, 2014) or of erotic pictures (Schomberg, Schöne, Gruber, & Quirin, 2016) on EEG. While both Hahn et al. (2016) and Trujillo et al. (2014) did not report differences exclusively for attractive faces, in Trujillo et al. the attractive faces had similar effects on the face-specific N170 as the averaged faces (compared to the low attractive faces). This is not surprising since averaging can make faces seem more attractive. Additionally, in the supplement material (Trujillo

et al., 2014) a largest P2 for attractive faces was reported. In Hahn et al. (2016), there were still effects of face esthetics and the age of the faces on ERPs. Although there were no effects reported for erotic pictures in Schomberg et al. (2016), they cannot be excluded since highest P1 amplitudes for erotic stimuli seem visible but were not statistically tested. Also, the effect of erotic pictures on alpha asymmetry was not observed in some studies (Uusberg et al., 2014; Wiedemann et al., 1999).

A big challenge lies in summarizing this heterogeneous group of studies. Within the 127 studies on cognition and sexual arousal only 33 accounts were found where statistical effect sizes were reported. These effect sizes relate to a multitude of different EEG measures (P1 amplitude, P1 latency, N1 amplitude, etc.) that cannot be compared. Within these 33 studies, the most frequently reported ERP components with effect sizes are the P3 and the LPP. Among the effect sizes for the P3 and the LPP only the ones from one-way repeated-measures ANOVAs with any sort of sexual stimulation as a factor level were selected. This resulted in 8 effect sizes for the P3 and the 17 effect sizes for the LPP. The results for the P3 ($N=300$) (see Fig. 1) seem unaffected by publication bias, as can be seen by the symmetrical funnel plot (see Fig. 2). Cohen's d effect sizes for the association between sexual stimulation and the P3 were 1.82 (95% CI 1.36–2.28) with 80.3% of variation across estimates being attributable to heterogeneity ($I^2=80.3\%$, $p<.001$). The results for the LPP ($N=510$) (see Fig. 3) are less clear and could be influenced by publication bias since the funnel plot (see Fig. 4) and the Egger's test ($p<0.001$) show that the large effects are from studies with smaller samples. Cohen's d effect sizes for the association between sexual stimulation and the LPP were 2.3 (95% CI 1.80–2.79) with 89.7% of variation across estimates being attributable to heterogeneity ($I^2=89.7\%$, $p<.001$).

The studies included using the criteria mentioned still show differences in their methodology. Therefore, the results should be interpreted with caution. While most included studies used visual stimulation, Lübke et al. (2012) used olfactory stimulation. Also, within the studies using visual stimuli different visual contents have been used (e.g., attractive faces in Wiese et al., 2014, naked bodies in Hietanen et al., 2014). In Hahn et al. (2016), the sexual stimulation contains only esthetic faces, but these faces were also rated as more attractive than the less esthetic faces. In Kuhr et al. (2013), the P3 and LPP results were identical; therefore, we included this effect size in both the P3 and the LPP analyses. For the meta-analysis of the LPP both effects on LPP and LPC were aggregated across studies. The main limitation of the calculations presented here is the potentially different cognitive processes that the components could represent across studies. Most studies measured the P3 and LPP during viewing of visual sexual stimuli. However, this (mostly) passive viewing was followed by different kinds of rating tasks

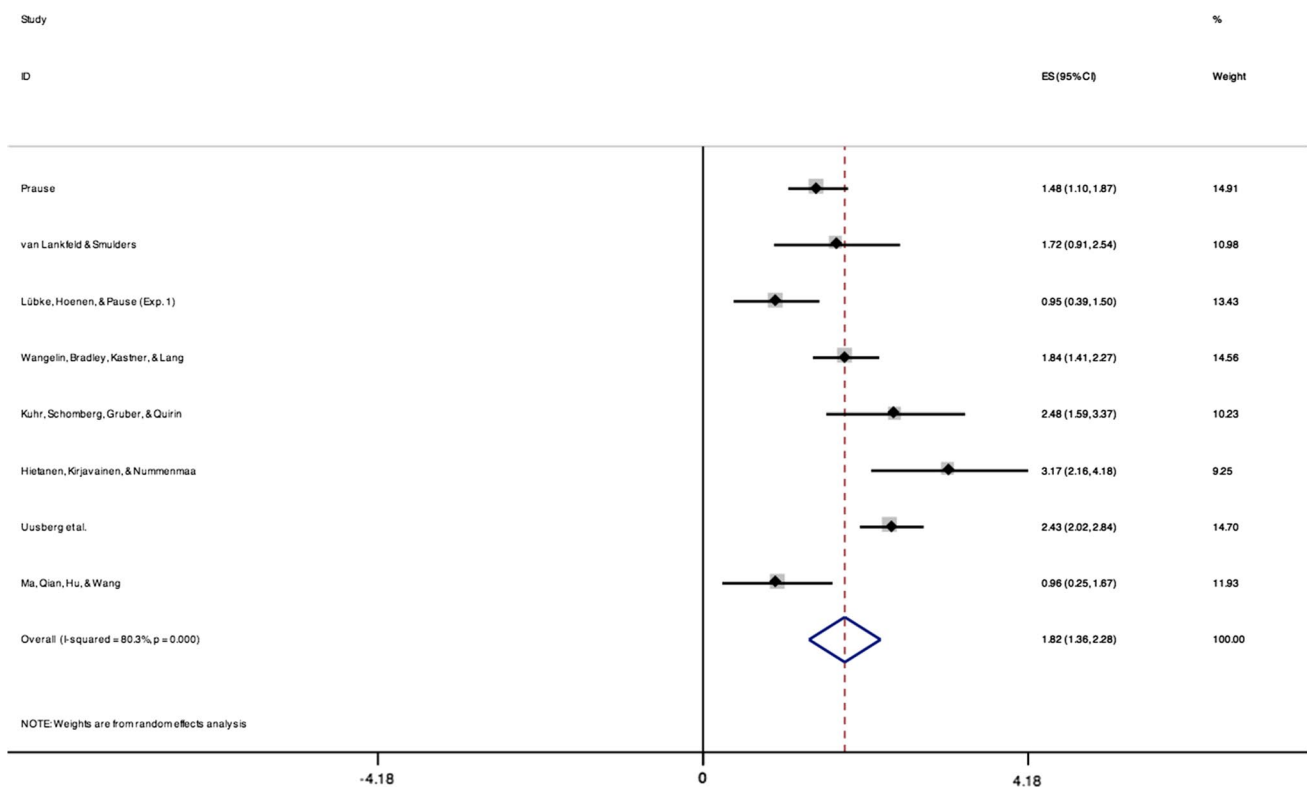


Fig. 1 Meta-analysis of the association between sexual stimulation and the P3

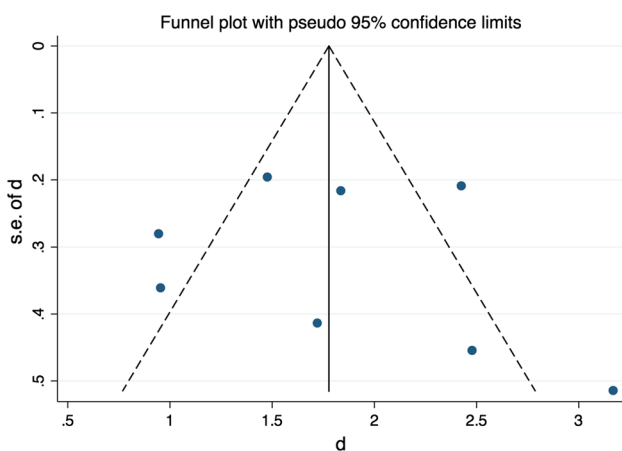


Fig. 2 Funnel plot for the meta-analysis of the association between sexual stimulation and the P3

and therefore with different emotional dimensions in mind. Participants could have different expectancies or mindsets during the ERPs due to different experimental frameworks (e.g., in Wangelin et al., 2012, the P3 represents a reaction to an acoustic startle stimulus during an erotic scene while in Ma et al., 2017b, the P3 during the presentation of an attractive face could also represent considerations within the ultimatum game of the study).

Neuroelectric Differences in Abnormal Sexual Preferences

The subject of sexual deviance has been mostly neglected in studies recording neuroelectric signals. Two studies linked the P3 in a visual oddball task to an onset of sexual behavior at such an early stage that it is considered as socially deviant (Iacono, Malone, & McGue, 2003; Iacono & McGue, 2006). A number of studies have also looked at victims of sexual abuse (e.g., Ben-Amitay, Kimchi, Wolmer, & Toren, 2016; Ito, Teicher, Glod, & Ackerman, 1998). A very small number of studies (16) looked at the neuroelectric recordings from individuals with abnormal sexual preferences (for an overview on mostly epileptic cases, see Temin & Mukhin, 1991). These studies mostly resemble the neuroscientific experiments mentioned above but with samples of exhibitionists, pedophiles, and sex offenders, including a multitude of different abnormalities. In general, the individuals diagnosed with various kinds of paraphilias were compared to healthy controls (see Table 6). In two systematic studies, no control group was used at all (Cassens, Ford, Lothstein, & Gallenstein, 1988; Corley, Corley, Walker, & Walker, 1994). Furthermore, in one study only the findings of visual inspections of clinical EEGs are mentioned for two pedophile cases (Berlin, 1983).

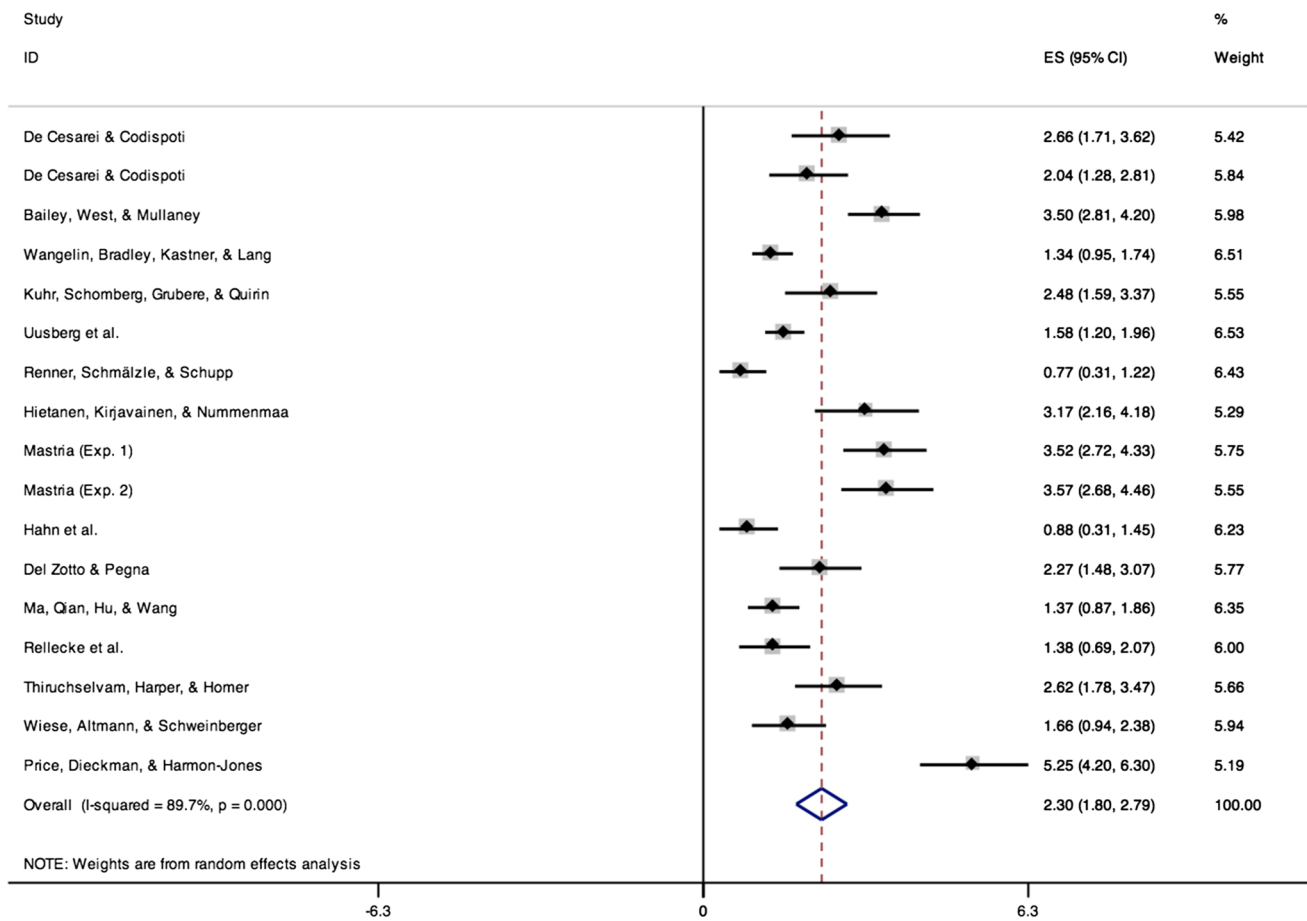


Fig. 3 Meta-analysis of the association between sexual stimulation and the LPP

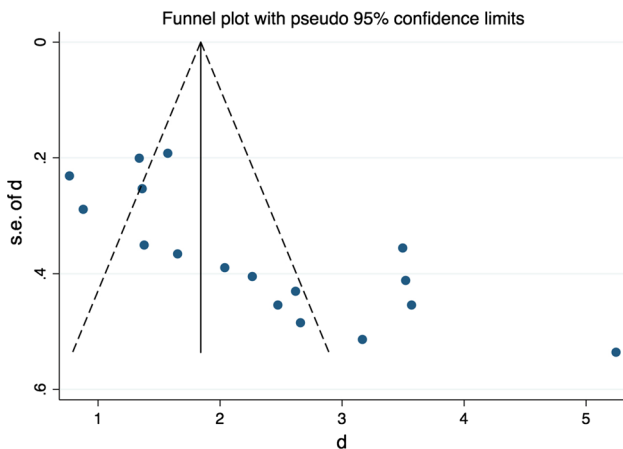


Fig. 4 Funnel plot for the meta-analysis of the association between sexual stimulation and the LPP

The earliest experiments were conducted in Germany and have widely been neglected by later authors. To our knowledge, Emrich (1978, 1979) was the first one who analyzed the ERPs of sexual offenders and compared them with

ERPs obtained from healthy controls. Sexual offenders were divided into a group showing long viewing times to pictures of sexual delinquency and to a group displaying shorter viewing times. Unexpectedly, only the group showing short viewing times was differentiated from the group of healthy controls using ERPs. In another experiment by Emrich, pictures of the same-picture categories were shown either subliminally or supraliminally. In this experimental setup, some sexual offenders showed higher ERPs to delinquency-related pictures although the results were not particularly consistent. Despite these somewhat inconclusive results based on visual inspection of the ERPs, the studies by Emrich employed a methodology and experimental designs that hold up to this day. Comparable luminance of the picture categories was ensured, control groups were included, and picture content was matched to the individual sexual deviations of the delinquent participants.

Later studies were based on the notion of hemispheric asymmetries brought about by cerebral lesions as a likely cause for all kinds of sexual preference disorders (Flor-Henry, 1980). Based on hemispheric localizations in large samples of epileptic cases with various forms of sexual abnormalities

(e.g., Kolářský, Freund, Machek, & Polak, 1967), lesions in the temporal lobe were assumed to disturb the dominance relationship between the two hemispheres resulting in dysfunctional overcompensations or inhibitions of one or the other hemisphere. In a review (Lang, 1993), pathology in the left temporal lobe in sex offenders was also highlighted. These assumptions were followed by a series of experiments in which potential structural differences in both hemispheres between sexual abnormal and normal samples were investigated using either resting state EEG or cognitive tasks that were supposed to activate either the left or the right hemisphere only. In this regard, the studies on interhemispheric differences in terms of abnormal sexual preference are similar to the work by Wegesin (1998) and by Alexander and Sufka (1993) on the normal variants of sexual orientation (i.e., differences between hetero- and homosexual individuals). In such studies, no sexual stimulation was used (e.g., by virtue of pictures with deviant content) to trigger brain waves representing sexual preference toward that content. The majority of studies on abnormal sexual preferences (9/16) fall into this category. Initial studies distinguished (discriminant function analysis on frontal alpha [78.9% correct classification] and theta [81.6% correct classification] power ratios [left/right] during block design task) exhibitionists from normal controls using differences in anteroposterior coherence (Flor-Henry, 1987; Flor-Henry, Koles, Reddon, & Baker, 1986) and in frontal alpha and theta activity (Flor-Henry et al., 1986). Later, an increased average activity during rest and reduced coherence during vocabulary and word fluency task in exhibitionists compared to controls was found (Flor-Henry, Lang, Koles, & Frenzel, 1988). Those studies (Flor-Henry, 1987; Flor-Henry et al., 1988) used large samples and suitable controls but differed highly in EEG settings (e.g., distance between electrodes or electrode reference) and in terms of statistical analysis (Flor-Henry et al., 1988). Additional differences become apparent in the results. While Flor-Henry (1987) and Flor-Henry et al. (1986) found most differences during visuospatial tasks, Flor-Henry (1988) reported no differences during that task. Using a much smaller sample and no control group, Cassens et al. (1988) reported decreased delta activity and unspecified abnormalities in left and right frontal sites in paraphilics. In a description of 23 pedophilic cases, Berlin (1983) mentioned EEG abnormalities in a homosexual pedophile and slow delta waves as well as frontal sharp activity in another homosexual pedophile. In a more systematic study with pedophilic subjects, Flor-Henry, Lang, Koles, and Frenzel (1991) found reduced interhemispheric and increased intrahemispheric coupling as well as increased frontal activity (alpha, delta, theta) in pedophiles. More such studies (Baker, 1985; Batamirov, Vvedensky, Tkatchenko, & Perezhogin, 1997; Corley et al., 1994; Ivashchenko, Eliseev, Tkachenko, & Petina, 1996; Kirenskaya-Berus & Tkachenko, 2003) again used different ways to calculate indexes of

coherence measures. Taken together, results presumably associated with sexual preference disorders were reported in many different frequency bands and at virtually all EEG sites with contradicting results. The most consistent results were reported for hemispheric asymmetries, primarily in the alpha range.

A couple of ERP studies used sexual imagery that matched particular abnormal sexual preferences (Howard et al., 1994; Waismann et al., 2003) and compared the CNV to controls. Group differences were more apparent when very small subsamples with more extreme values in self-report measures on sexual preferences were selected. Larger CNVs to female adults than to female children were observed in controls, while no such difference was measured in pedophiles (Howard et al., 1994). The P600 in response to paraphilic pictures differentiated paraphiles from controls more clearly and also correlated with self-reports on sexual preferences in both groups (Waismann et al., 2003). In a recent ERP study with pedophilic participants, no child stimuli were used but only images with normal erotic content involving adults (Knott et al., 2016). Again, controls showed higher early ERPs (P2, N2) in frontal sites for the erotic pictures than for all the other picture categories. The amplitudes for erotic pictures were more pronounced in the healthy controls than in pedophiles as was shown by an interaction of group and picture category. Moreover, the ERP signals to erotic pictures at the earliest time point, where disparities between ERP waveforms toward normal and erotic pictures were significantly different between the groups, correlated inversely with values on the Bumby MOLEST Scale (Bumby, 1996), a self-report questionnaire on sexual abuse against children. Flor-Henry et al. (1991) had already remarked on a failure to respond to normal sexual stimuli in paraphilics, and these subsequent ERP studies (Knott et al., 2016; Waismann et al., 2003) seemed to support this response deficiency theory.

Disturbances in Sexual Behavior

Apart from normal genital function and cognitive aspects of sexual arousal in healthy subjects and in abnormal sexual preferences, a number of studies have focused on sexual behavior under several other clinical conditions or disorders of the nervous system affecting the genitalia or sexual behavior. Apart from systematic studies, case reports have been published on several issues.

Sexual Seizures in Epileptic Patients

EEG recordings have been used intensively in the area of epilepsy. Accordingly, the rare cases, where manifestations of epileptic discharges take the form of sexual behaviors, have eventually captured the interests of clinicians employing EEG methods. EEG methods in epilepsy often rely on

continuous recordings of longer time periods, sometimes done repeatedly in multiple sessions. Visual inspection is used to track discharges, spikes, slow waves, etc., for classification of seizures, localization of the epileptogenic zone or to make preparatory examinations for surgery (Noachtar & Rémi, 2009). Thus, the case reports mentioned here did not solely focus on human sexual functions but had more practical clinical goals with less theoretical conceptualizations.

In the literature, sexual seizures have been mentioned long before the advent of EEG. As mentioned before, Democritus (as cited in Kinsey et al., 1953) had already compared epileptic seizures with orgasm. In modern times, there have been speculations about a causal relation between epileptic discharges and sexual repulsions or habits (e.g., Epstein, 1969). In this field, clinical EEG was mostly used during rest, ictal, or interictal phases to localize the epileptic focus through spike activity on the scalp. Appropriate technological necessities for the storage of EEG data for further quantifications was not available at the time of the early reports. (Such non-quantitative approaches are still used in modern neurology.) Sometimes electrodes were also implanted intracranially for invasive mapping. All these procedures are often described in clinical reports with minimal mention on apparatus settings and relying mostly on visual inspection of EEG waves. Many forms of sexual activities used to be considered as deviant (for a historical review, see De Block & Adriaens, 2013) and, if present, epilepsy was assumed to be the cause of such deviant activities even when they occurred outside of seizures. Table 7 lists case reports describing EEG recordings in epileptic patients with sexual abnormalities or behavior that was considered as abnormal. Although this includes expressions of the opposite gender, sometimes occurring with the onset of epilepsy (Davies & Morgenstern, 1960), cases where transgender and transsexualism was researched outside of epileptic samples are excluded (e.g., Flor-Henry, 2010; Wälinder, 1967) from the present review. Similarly, homosexual behavior that used to be regarded as aberrant in earlier times is not considered within this review in connection with epilepsy or other neurological disorders. At this point, it should be stressed that homosexuality is not considered as abnormal or deviant in any way. EEG recordings made with epileptic patients were sometimes used to derive assumptions about brain activity as related to sexual behavior (for a summary of several cases of sexual seizures, see Temin & Mukhin, 1991, in women, see Rémillard et al., 1983; for orgasmic seizures, see Janszky et al., 2002; for expressions of the opposite sex, see Hill, Pond, Mitchell, & Falconer, 1957; and for fetishistic cases, see Epstein, 1960).

Although the case by Erickson (1945) mentioned above described epileptic seizures resulting in hypersexual tendencies, no EEG was recorded in that patient. The earliest report on EEG in connection with epilepsy and sexual behavior involved the case of a 44-year-old woman suffering from

epileptic seizures and experiencing sexual feelings similar to being shortly after orgasm (Bente & Kluge, 1953). These feelings occurring intermittently during sleep were described “as if her husband was just with her” (Bente & Kluge, 1953, p. 363), but had a sense of shame and strangeness to them. Visual inspection of the EEG during resting state showed discontinuous low amplitude alpha waves and one spike indicative of temporal left epileptic focus. Two similar cases involving orgasmic seizures and genital sensations (“tingling” p. 488, in testes) were reported subsequently (Mulder, Daly, & Bailey, 1954) and another 25 cases (out of 36) with further EEG recordings and sexual abnormalities (Gastaut & Collomb, 1954). According to the literature, a diverse spectrum of highly varying sexual behavior was observed in epileptic patients. This includes seizures associated with sexual arousal, seizures induced by orgasm, fetishistic behavior, voyeurism, exhibitionism, sexual verbalizations, and hypersexuality (including aggressive and bizarre sexual advances), but also hyposexuality, sexual repulsion, impotence as well as seizures with genital sensations, genital automatism (defined as “repeated fondling or grabbing of the genitals” p. 1188, Leutmezer et al., 1999), and genital pain, or seizures with putative links to activities of the opposite gender (see Table 7). There was also one report of a seizure patient suffering from sexual precocity (Money & Hosta, 1967). Therefore, a systematic relationship between neuro-electric signals and sexual abnormalities could be found in the collected EEG recordings and patient observations. From early on, it was assumed that discharges originating from the rhinencephalon, involved in central emotional functions and expressions (Papez, 1937; Terzian & Ore, 1955), spread through the temporal lobe and lead to modifications of a subject’s emotional behavior. Stimulations of the temporal cortex had been shown to reproduce events from memory along with the emotions attached to that event (Penfield, 1952). An inability to recall the events surrounding a sexual seizure had also been observed. The temporal lobe and its role in the storage of emotional experience were therefore frequently discussed throughout most reports and later associated with regulations of sexual arousal (Epstein, 1961).

In one 14-year-old male epileptic patient with exhibitionism, voyeurism, and opposite gender expressions, spikes and high-voltage potentials were recorded in the right hemisphere predominantly (Petritzer & Foster, 1955). Two similar cases showed discharges and alpha spiking in the left hemisphere (Bhaskaran, 1955). Bhaskaran regarded the psychosexual misidentification of the patients resulting in impotence as potentially relevant for their epileptic attacks. In a more famous case, Mitchell, Falconer, and Hill (1954) described an epileptic patient with seizures triggered by the object of his fetishistic preference (safety pin). While exposed to the object, the EEG showed frequent firing in the left frontotemporal region leading to a fit 30–40 s later. This was followed

by left frontotemporal high-voltage slow waves with irregular changes. After anterior temporal lobectomy, the fetishistic preference was alleviated. Moreover, Mitchell et al. described the patient's EEG activity as innocuous when he was confronted with the object in question, but with the exception of an occasional low-voltage spike in the left mid-temporal area (near operation site). Temporal lobectomy was also reported to alleviate an abnormal sexual preference in a 13-year-old boy with EEG abnormalities in the left inferior temporal lobe (Pond & Bidwell, 1954). Both the case of Pond and Bidwell (1954) and the case of Mitchell et al. (1954) were later reported again by Falconer et al., (1955) with the addition of three new cases (Case 3: hyposexuality; Cases 8 and 21: exhibitionism) of epileptic patients with sexual abnormalities displaying a spike or sharp-wave discharging focus in bilateral temporal regions and in the left anterior temporal region. In another case, bilateral temporal lobectomy led to changes in sexual behavior as the patient developed exhibitionism and hypersexuality (Terzian & Ore, 1955). Since temporal lobectomy led to changes in sexual activities, the focus was laid on temporal lobe epilepsy and its relation to sexually deviant behavior (Hill et al., 1957). In a larger sample of male epileptic patients, countless forms of sexual deviation were indeed linked to temporal lobe epilepsy (Kolářský et al., 1967). Although there have been numerous reports linking temporal lobe epilepsy to sexual abnormalities and assumption about the role of gender and temporal lobe hemisphere (left or right) within those abnormalities were stated, the results are not always consistent. Furthermore, some studies only reported vaguely on minimal sexual abnormalities in patient samples and found some EEG alterations only after administration of substances (e.g., scopolamine alpha chloralose: Monroe, 1959; Monroe, Jacobson, & Ervin, 1956). In one further surgical patient without seizures, spikes and slow waves in the anterior temporal lobe during resting state were recorded (Ostow, 1954). Although the patient was described as having obsessional thoughts with embarrassing and affective content, it is unclear whether this had any sexual relevance.

Both hyper- and hyposexuality in epileptics were associated with an epileptic focus in the anterior temporal lobe (Blumer, 1970). Temporal lobe epilepsy was linked to hyposexuality (Shukla, Srivastava, & Katiyar, 1979) with studies highlighting the role of the left temporal lobe (e.g., Falconer et al., 1955) and occasional reports on the right temporal focus (e.g., Gastaut & Collomb, 1954; Trevisol-Bittencourt & Troiano, 2000). Hyposexuality and spike activity were reversed in one study after temporal lobectomy (Blumer & Walker, 1967). Impotence was similarly linked to abnormalities in frontotemporal sites (Hierons & Saunders, 1966) but also to left and right temporal spikes (Bhaskaran, 1955; Johnson, 1965). Seizures taking the form of sexual arousal have also been attributed to EEG abnormalities in both temporal

hemispheres (Rémillard et al., 1983). Right temporal epileptic focus in epileptics was also associated with hypersexuality (Torelli & Bosna, 1958) also in form of urges and genital secretion (van Reeth, Dierkens, & Luminet, 1958). Parietal sites were also associated with hypersexuality (Grabowska-Grzyb, Nagańska, & Wolańczyk, 2006). There have also been reports on more sexually aggressive behavior like sexual attacks in crowded streets with relation to temporal lobe epilepsy (Hosseini, Yassini, & Nadi, 2013) or an attempt to have intercourse with one's sister 6 (years of age) linked to left temporal spiking (Walker, 1972). Less aggressive behavior (reaching toward groin of the EEG technician) was linked to left anterior temporal spiking (Currier, Little, Suess, & Andy 1971). Temporoparietal abnormalities were further associated with sexual verbalizations (Freemon & Nevis, 1969).

Within orgasmic seizures, there were cases in which orgasm was induced by seizures (Terzian & Frugoni, 1958), where seizures were induced by orgasm (Hoenig & Hamilton, 1960; Ozkara et al., 2006; Sengupta, Mahmoud, Tun, & Goulding, 2010), where orgasmic seizures were brought about by brushing teeth (Chuang, Lin, Lui, Chen, & Chang, 2004), or where seizures led to ejaculation without erection (Bachman & Rossel, 1984). In one patient, hyperextension of his back led to seizures with sexual pleasure that would not be triggered by regular intercourse (Jacome, McLain, & Fitzgerald, 1980). Orgasmic seizures were experienced as fearful by some patients (Ruff, 1980; Walker, 1972) or as both pleasant or painful by others (Calleja, Carzipo, & Berciano, 1988). Orgasmic seizures were linked to bitemporal (Dobesberger et al., 2004; Patarnello, 1963; Tanuri, Thomaz, & Tanuri, 2000), left (Amâncio, Zymberg, & Chiari Pires, 1994; Case 7: Janszky et al., 2004), and mostly right abnormalities (Crevenna, Homann, Feichtinger, Ott, & Körner, 2000; Gautier-Smith, 1980; Janszky et al., 2002, 2004), but also to non-lateralized temporal theta activity (Aull-Watschinger, Pataraiia, & Baumgartner, 2008), or frontotemporal epileptic focus (Reading & Will, 1997). Intracranial recordings have also shown the involvement of the amygdala and the hippocampus (Bancaud et al., 1970; Surbeck et al., 2013). With these seizures, however, there is often a parietal shift reported for the spikes (e.g., right parietal focus; Ruff, 1980). One patient showed spike focus at the vertex and experienced sensations similar to orgasms, seizures with genital sensation, and paresthesia bilaterally in the clitoris (Kennedy, 1959). In this patient, a meningocerebral cicatrix was located in the upper part of the central fissure where the genitalia are assumed to be represented. Discharges near the paracentral lobe were also linked to sudden erections in one patient (Stoffels, Munari, Bonis, Bancaud, & Talairach, 1980). Other cases showed no EEG abnormalities (Berthier, Starkstein, & Leiguarda, 1987), but the seizure induced by orgasm was experienced unilaterally on the left-hand side and a CT scan revealed a lesion situated in the right paracentral

lobule and the precentral gyrus. In contrast, another case showed no structural lesions as measured by MRI or CT (Crevenna et al., 2000). Genital automatisms were also associated with bitemporal spikes (Leutmezer et al., 1999), ictal events in orbitofrontal regions (Spencer, Spencer, Williamson, & Mattson, 1983), or temporoparietal abnormalities (Freemon & Nevis, 1969). In these cases, patients had no recollection of their behavior afterward (Currier et al., 1971; Freemon & Nevis, 1969). Also, genital automatism sometimes involved grabbing of genitals without any sexual feeling (frontal and parietal abnormalities; Geier et al., 1975, 1976) or genital pain (York, Gabor, & Dreyfus, 1979).

More deviant behavior in relation to temporal lobe spikes was shown through episodes of undressing and behavior in a “coy, bizarrely seductive fashion” (p. 491: Ervin, Epstein, & King, 1955) and opposite gender expressions and fetishistic behavior with left anterior temporal lobe abnormalities (Hunter, Logue, & McMenemy, 1963). Exhibitionism in epileptic patients was also linked to left temporal spike focus (Hooshmand & Brawley, 1969). In contrast, other case reports found no EEG abnormalities in an epileptic patient with fetishism (Ball, 1968). In one epileptic patient with opposite gender tendencies, no EEG abnormalities were reported except a singular spike from the right temporal region but in other cases abnormalities in both or only within the right temporal region have been described (Davies & Morgenstern, 1960). Further opposite gender expressions and fetishistic behavior in epileptic patients but also in non-epileptics was again linked to right and left temporal spike focus (Epstein, 1961). Transsexual epileptics sometimes show EEG abnormalities in form of asymmetries (Hoenig & Kenna, 1979).

Even after many reports on sexual seizures and their variability, the exact mechanisms are not completely clear. Apart from emphasizing the role of the right temporal cortex and giving a more detailed spatial description of the brain regions involved (e.g., Surbeck et al., 2013), new theoretical explanations have rarely been posed. For some forms of sexual seizures, a categorization into focal and reflexive seizures has been suggested (Xue & Ritaccio, 2006), if they are induced by somatosensory influences.

Sexual Behavior During Sleepwalking

Within parasomnia (sleepwalking), rare cases of atypical sexual behavior have been reported during episodes of sleepwalking. The term “sexsomnia” (p. 311) has been proposed as a specifier within the diagnosis of sleepwalking for this behavior (Shapiro, Trajanovic, & Fedoroff, 2003). The condition is found as a variant of non-rapid eye movement (NREM) parasomnia in classification systems (American Academy of Sleep Medicine, 2014). A number of reviews have summarized different aspects of this condition (Andersen, Poyares, Alves, Skomro, & Tufik, 2007; Organ & Fedoroff, 2015;

Schenck, Arnulf, & Mahowald, 2007) which is also referred to as “sleepsex” or “somnambulistic sexual behavior” (p. 272: Andersen et al., 2007). Neuroelectric findings are summarized in Table 8. Episodes of such sexual behavior during sleepwalking episodes have been characterized as strange, disturbing, and harmful, often involving violent acts against others, usually the bed partner, or against oneself while the acting person is in an unresponsive or confused state with no later memory of the event. The acts in question involve sexual intercourse, verbalizations, masturbation, moaning, or sexual assault and may also result in harmful sequelae for the patient’s own emotional well-being since awareness of such acts is accompanied by shame and guilt. Frequently, such behavior is followed by criminal charges from victims of the sexual assaults. While such episodes have been described since 1897 (exhibitionism in a “state of stupor” and with no later memory of the event was described as an attack of “nocturnal somnambulism” pp. 376–377: Thoinot, 1911) only in recent decades have such patients been studied with modern neuroscientific methods. Table 8 lists case reports, where neuroelectric measurements were conducted with patients suffering from episodes of sexual behavior in their sleep. Apart from EEG, such investigations often employ the entire polysomnographic setting during sleep to construct hypnograms.

EEG during wake resting state in such patients mostly showed no abnormalities, and sleep EEG was also normal in many cases. Often the polysomnographic setting was brought to the patient’s bed at home to conduct the sleep study with more habitual sleeping patterns than can be expected in laboratory settings. Such recordings are usually done on multiple occasions, while the EEG is used to categorize different sleep stages occurring during sleep cycles. The most common findings from such recordings in sexsomnia patients show abrupt, spontaneous, and frequent arousals from slow-wave sleep stages and hypersynchronous delta wave patterns. The findings generally overlap with findings indicative of sleepwalking (Blatt, Peled, Gadoth, & Lavie, 1991; Schenck, Pareja, Patterson, & Mahowald, 1998) as pointed out elsewhere (Ebrahim, 2006). The delta wave pattern observed right before episodes, the rise in alpha activity during episodes with persisting delta activity match the light sleep/wake transitions in which episodes were observed (Cicolin et al., 2011). Again, EEG can be highly contaminated by movement artifacts during such episodes. Rapid eye movement (REM) activity resembling the awake state with desynchronous EEG is characterized by the presence of eye movement, while other muscles are paralyzed, hindering intended movements. This is somewhat in line with the categorization of sexsomnia as a NREM parasomnia, since during the NREM stage more slow waves are present and muscle activity is only reduced. Yet episodes of sexsomnia have also been observed during the REM stage (Guilleminault, Moscovitch, Yuen, &

Poyares, 2002) and sexual function in form of erections also occurs during this sleeping stage (Karacan, Goodenough, Shapiro, & Starker, 1966).

So far, more male cases have been reported. The sexual behavior reported, which also happened during daytime napping (Pelin & Yazla, 2012), included masturbation and intercourse but also violent masturbation of partner (Béjot et al., 2010) or self (Guilleminault et al., 2002). More aberrant acts involved loud sexual moaning (Guilleminault et al., 2002), fondling of a young girl (Cicolin et al., 2011), sexual touching of own daughter, of a relative's testicles (Shapiro et al., 2003), and rape (Ebrahim, 2006). In one case, it involved the downloading of male pornography (Shapiro et al., 2003). Apart from abnormal sexual behaviors, one patient, described as “different person” when engaging in sexual intercourse during sleep, was also reported as more “gentle,” “amorous” and more concerned with the partner sexual satisfaction during episodes than when he was awake (p. 313: Shapiro et al., 2003). During episodes, patients were depicted by witnesses to be “glassy eyed” (p. 526: Cicolin et al., 2011), have a “glazed look” (p. 220: Ebrahim, 2006), or to be “far away” (p. 331: Guilleminault et al., 2002). They were not able to recognize own family members (Pelin & Yazla, 2012) and were sometimes stoppable (Cicolin et al., 2011) but in other instances described as unstoppable (Pelin & Yazla, 2012). In some cases, waking up required shaking or a hard slap (Shapiro et al., 2003). Once awoken, the behavior stopped (Shapiro et al., 2003) and patients seemed disoriented and confused or even upset, sometimes accusing the partner of sexual coercion (Guilleminault et al., 2002). Patients were not able to remember the episodes nor recall it as a form of dream in any reported case. Sometimes doubt on the occurrence was stated (Guilleminault et al., 2002). These episodes seemed to influence daily awake behavior in one case where an increase in libido and a clear change in behavior were observed coinciding with the onset of episodes of sexsomnia (patient started asking random women for sex; Pelin & Yazla, 2012).

Theoretical explanations for such sexual acts originated from dream theories often hinting at a form of inner conflict resolution (Bornemann, 2013). Modern approaches have largely highlighted the role of sleep deprivation, stress, and excessive fatigue, while the role of alcohol is still debated (Pressman et al., 2012). Physical contact in bed appears to be a provoking factor in some cases, and it still remains unclear how reliably the cause of sexsomnia can be identified using PSG and clinical evaluations (Schenck et al., 2007).

Neuroelectricity and Changes in Sexuality

In the surgical studies mentioned in the Section “[Electrophysiological Localization of Genitals in the Human Brain](#)” with regard to longer-lasting effects (Castelli et al., 2004;

Hariz et al., 2008; Hwynn et al., 2011; Merola et al., 2017; Mock et al., 2016; Roane et al., 2002; Romito et al., 2002; Serranová et al., 2013; Teive et al., 2016; Temel et al., 2004; Visser-Vandewalle et al., 2003a, b, 2005), sexual behavior was influenced incidentally using DBS. Thus, the results were always reported as unintended side effects. Other studies used electrical stimulations and induced orgasms only because they triggered the kind of orgasmic seizure that the patient usually experienced. There are, however, studies in which the goal of the endeavor was to enhance, to reduce, or to change sexual behavior or arousal (see Table 9). These objectives range from modifying related reactions noninvasively and short term within experimental settings to attempts at inducing long-lasting changes in sexual preference through invasive stimulation of the brain.

Pharmacologically induced changes were examined in three studies. Wacker et al. (2013) used a selective dopamine-D2-receptor blocker (sulpiride pill, 200 mg) in a male sample 3 h before an EEG recording and observed an association between higher left–than right frontal alpha activity and higher approach motivation scores, while the placebo group showed the reverse pattern (higher approach motivation scores related to higher right–than left frontal alpha activity). These differences in alpha asymmetry were only observed if the female experimenter was attractive, while no differences were present with an unattractive female experimenter. Although the relationship between dopamine and frontal alpha asymmetry in that sample was also shown through Val158Met polymorphism of the catechol-*O*-methyltransferase gene (Val/Val carriers showed higher asymmetry scores than Val/Met or Met/Met carriers), which is assumed to play a role in prefrontal dopamine availability (Tunbridge, Bannerman, Sharp, & Harrison, 2004), the pharmacological manipulation of frontal alpha asymmetry via the dopamine route was only observed when the context was sexual. Using a selective serotonin reuptake inhibitor (sertraline, 50 mg), also used for treating premature ejaculation (McMahon, 1998), 4 h before EEG recordings, Lee et al. (2010) inhibited the effects erotic films have on current source density (high beta frequency in the middle frontal gyrus, the precentral gyrus, the postcentral gyrus, and the supramarginal gyrus). While the current source density measures did not differ between sertraline and placebo condition during the presentation of a music clip, for the erotic film sertraline induced an increase in high beta frequency in the left precentral gyrus, the inferior, middle and superior frontal gyrus, cortical areas associated with self-control (Hare, Camerer, & Rangel, 2009; for additional results in the right medial frontal gyrus, see Kwon et al., 2011). Such cortical areas were also targeted with TMS in Prause et al. (2016) to examine EEG signals related to sexual reward in form of genital vibration. Based on findings by Di Lazzaro et al. (2005), cortical activity can be increased with intermittent

theta burst stimulation (iTBS), while continuous TBS (cTBS) should decrease cortical excitability. Prause et al. (2016) used 3 TMS pulses (50 Hz) every 200 ms (5 Hz) to deliver iTBS (2 s train every 10 s with total of 190 s = 600 pulses) as well as cTBS (40 s train, uninterrupted TBS = 600 pulses). iTBS reduced alpha activity in anticipation and reception of sexual reward when compared to cTBS. This alpha suppression was more pronounced during anticipation than during reward. When the reward was monetary instead of sexual TBS did not affect alpha activity. In sum, the experimental influences were only detectable when a specifically sexual context made them apparent in the pharmacological studies as well as in the TMS study. While TMS had an effect on the left DLPFC, transcranial direct current stimulation (tDCS, 2 mA, 20 min) had an effect on the right DLPFC (Ferrari et al., 2015). tDCS selectively influenced attractiveness ratings for facial stimuli. Other case reports mention the usage of TMS (Tripathi, Singh, Singh, & Kar, 2016), electroconvulsive therapy (ECT; Korda, Pfaus, Kellner, & Goldstein, 2009) and with no success tDCS (Morin et al., 2017) in treatment of genital and sexual disorders. TMS and ECT reduced symptoms of hypersexuality and persistent genital arousal disorder (Korda et al., 2009; McMullen & Agarwal, 2016; Tripathi et al., 2016; Yero, McKinney, Petrides, Goldstein, & Kellner, 2006) although sometimes this was followed by relapse (Korda et al., 2009) and the effect was absent in other cases (Eibye & Jensen, 2014).

The most controversial works were reported in the 1970s by Heath (1972) and by Moan and Heath (1972). In their stimulation experiments with single subjects, they focused on the modification of sexual arousal in patients. In one 24-year-old male patient suffering from temporal lobe epilepsy, chronic depression, and suicidal risk with deficits in experiencing pleasure and a history of drug abuse, the patient's homosexuality was also frequently mentioned in the case description. They described also bitemporal slow-wave activity (maximal on the left) and paroxysmal delta activity in the right temporal area. Both activities were described as abnormalities during resting state EEG after chloralose. To improve the pleasure response, electrodes were implanted operatively inside the brain at multiple regions including the right mid-septal region. After initial periods of passive stimulations in septal regions, the patient reported improvement in mood and sexual motivation while EEG recordings were unremarkable. All stimulations were carried out with currents of 0.5–7.5 mA. The patient was also allowed access to the buttons for self-stimulation, which lasted 3 h longer than the passive stimulations probably due to the number of the button presses, resulting in “almost overwhelming euphoria and elation” (p. 27). Finally, the patient had to be disconnected against his protest. EEG after such sessions was again unremarkable. Although prior work by Heath (1964) implicated the septal region in sexual arousal, it is not stated why

the responses to stimulation of this region should produce a change in sexual orientation. Nonetheless, the treatment was used to initiate heterosexual behavior in this homosexual patient that had never engaged in heterosexual activities. To test the treatment efficacy, the patient was brought together with a female prostitute after days of stimulation sessions and engaged in sexual intercourse with her as had been expected by the authors. Further “progress” (p. 29) is mentioned in the form of a later sexual relationship with a married woman outside the laboratory. Another epileptic patient received acetylcholine in 12 occasions (400 mg, 70 lambda) and lev-arterenol bitartrate in four occasions (140 mg, 70 lambda) through intracortical cannulas that were implanted in the septal regions. This induced orgasm and EEG changes. Neither of the publications by Heath (1972) and by Moan and Heath (1972) mentioned any documentation of consent on behalf of the participants. Both of the experiments were carried out at Tulane University, presumably on contract to the U.S. Army and the Office of Naval Research (Ross, 2007). In addition, the EEG results reported were based on visual inspection; the patients were never quoted as stating any expression indicative of actual sexual pleasure. Alternatively, their behavioral descriptions may have been reduced to compulsions to engage in sexual activity or desires for more cortical stimulation without pleasure (Berridge & Kringelbach, 2008). Compulsive self-stimulations with intracranial electrodes have been also reported in a case where a patient was treated for chronic pain syndrome (Portenoy et al., 1986).

Discussion

The studies reviewed herein mirror the development of both research interests and methodological advances concerning the electrophysiology of sexual arousal, orientation, and preference. The size of the number of studies encountered within a specific topic varies largely. The same goes for the number of theory-driven approaches and the conceptual frameworks within a topic. The findings are by no means exhaustive, and it is likely that studies have been missed.

Neuroelectricity and Genital Physiology

The results of extant studies on somatotopic representations of the human genitals are not unanimous. Therefore, research in this domain is still ongoing. When localization is the primary goal, electrophysiology has been largely replaced by fMRI and MEG methods. fMRI and MEG offer higher spatial resolution than scalp potentials, are less invasive than in-depth recording or stimulation, and allow dispensing with a priori assumptions guiding the placement of electrodes (for a review, see Cazala, Vienney, & Stoléru, 2015). Intracranial methods for the invasive mapping of epilepsy vary

considerably in terms of the placement and number of electrodes. Consequently, it is difficult to compare the results of the corresponding studies. Still, one should concede some biological plausibility to the representation of genitalia in Penfield's homunculus (Penfield & Jasper, 1954) as based on the first electrophysiological measures despite the methodological advances over the last 64 years. The large sensory area compared to the small motor area associated with the genitalia was already in line with the minimal role of the motor cortex in penile movement, which is presumably mostly controlled by the autonomic nervous system and the primarily afferent fibers of the dorsal penile nerve. Advancements in research on genital representation have been summarized recently (Cazala et al., 2015). Latest assumptions incorporated evidence from brain imaging studies. fMRI signal has been linked to local field potentials (Logothetis, Auguth, Oeltermann, Pauls, & Trinath, 2001) as well as spiking activity (Lima, Cardoso, Sirotin, & Das, 2014). The medial and lateral surfaces of the primary somatosensory cortex seemed to be linked to representations of genitalia (Cazala et al., 2015). The insula as well as secondary somatosensory cortices were associated with the emotional aspects involved (Cazala et al., 2015). Analogous emotional aspects have been tackled in electrophysiological studies where cortical stimulation of the hippocampus led to abdominal sensations or feelings of "fluttering" and "butterflies" (p. 4: Van Buren, 1963) as well as epileptic sexual seizures described as "warm" (p. 325) or "vibrating" (p. 327) sensations in the stomach (Rémillard et al., 1983).

Results from studies using electrical stimulation on genitals can further add information for the localization of the genitals in the cortex. Since response maxima of genital stimulation or genital pain (York et al., 1979) were observed at the midline of the scalp (over the sensory cortex) and bit-mapped images showed symmetrical peaks culminating at Cz (Guérit & Opsomer, 1991), this was considered as consistent with the assumed sensory afferents of genitals in the midline of the interhemispheric fissure suggested by Penfield (Haldeman et al., 1982a). Later studies using not only medial electrodes as in Allison et al. (1996) but also lateral electrodes supported the view, however, that the fibers of the dorsal penile nerve project to a broader area in the primary sensory cortex and not only to the postcentral gyrus within the interhemispheric fissure (Bradley et al., 1998). Interestingly, in patients with erectile dysfunction, electrical stimulation of the penis did not lead to any recordable response on the scalp, although the stimulation was still visible at the spinal cord but only for the one patient with still intact nocturnal penile tumescence (Haldeman, Bradley, & Bhatia, 1982b). Future studies should focus on sexual arousal derived from such genital stimulations and try to relate the formation of sexual reward with properties of the nerves (e.g., increased axon density). Sexual arousal formed through genital stimulation

has been proposed as an essential factor for the development of sexual reward and incentive (Georgiadis & Kringelbach, 2012; Pfaus et al., 2012).

Regarding studies on orgasm and manual self-stimulation, EEG results need to be considered with caution, since EEG signals in such experiments are often contaminated by body movement. There is also a variability in how the stages of orgasm are identified ranging from observations to self-reports using a button press or vaginal blood flow. Comparability between EEG waves from orgasm and orgasmic seizures is also limited. The hemispheric asymmetry during orgasms that had been initially proposed (Cohen et al., 1976) was not replicated again in orgasm studies but in studies on nocturnal penile tumescence without orgasms. There, it was also only reported in the earliest studies. Technical settings and picture presentations from recent studies (Ponseti & Bosinski, 2010; Ponseti et al., 2009) coupled with modern preprocessing and artifact rejection methods can bypass many of the limitations from earlier studies, yet only a small number of such experiments, exclusively with male participants, have been reported.

Cognition and Sexual Arousal

The largest number of studies consists of EEG experiments conducted on human sexual arousal and cognition. The studies in this domain tackled many different aspects of human sexuality, even with new wavelet-based processing methods being evaluated for the processing of erotic stimuli (Rafiee, Rafiee, Prause, & Shoen, 2011). There are, however, several limitations, some of them typical of neuroscientific studies in general, to be taken into account. Apart from the small sample sizes oftentimes encountered in neuroscientific research (Button et al., 2013), the studies in question show great heterogeneity in several respects making direct comparisons between the studies or meta-analytic integration very difficult. Even though significant results for the same ERP components have been reported repeatedly, a closer look at experimental designs, tasks, instructions, samples, electrode placements, and statistics reveals that almost no study has been replicated in the exact manner. Furthermore, differences can be found in the type of stimuli used. It would be desirable that researchers made sure that the distinct stimulus categories used differed in terms of emotional valence, arousal, and urge not only prior to conducting the study but also for the individuals actually taking part in the experiment. In some studies, though, the emotional properties of the stimuli were only rated in a pilot, whereas in other studies the stimulus quality was not assessed at all. In addition, the mixture of modalities (auditory, visual, olfactory, or combinations thereof) and the duration of the stimulus presentation also varied across studies. Moreover, basic physical properties (contrast, luminescence, etc.) should be held constant across

different image categories and experimental conditions. This also applies to the number of pictures within a category since it effects signal-to-noise ratios when trials are averaged. Other problems arise from the selection and composition of the samples. Women and men experience sexual stimulation differently (e.g., Carvalho et al., 2013), and therefore, gender-adjusted sets of erotic stimuli should be used if possible. Handedness and sexual orientations were not always controlled. Presumably, the largest source of variation and the largest methodological problem lie in data preprocessing and analysis. While early researchers had no means of recording data for quantification digitally, modern EEG studies have abundant ways to evaluate data. In particular, ERPs allow for many more ways to arrive at significant results than most behavioral measures. This multitude of options, however, may attract problems of its own, such as *p*-hacking or voodoo correlations. Analysis of variance was by far the most frequently used statistical procedure in the studies reviewed here. The selection of time windows and electrode sites to calculate components for statistical analysis can be done in ways to maximize the degrees of freedom and thus to manipulate type I error rates. Ideally, the specifics of the analysis and the hypotheses should be stated before data collection, but some explorative approaches can be justified for tasks that have never before been combined with ERPs (Luck, 2014). It is important to separate results gained from such explorative procedures from the ones gained through analyses strictly driven by hypotheses. Helpful suggestions on the subject are provided by Luck and Gaspelin (2017). Future ERP studies on human sexuality ought to be considerate of such statistical problems since this poses a serious threat to conclusive results on the subject, but also to other ERP-related topics.

Apart from the high variability, some common trends can be seen in the results. Regardless of modality, erotic stimuli can mostly be differentiated from other emotional or neutral stimuli with EEG data, especially in tasks demanding visual attention. This was even observed in studies where the non-erotic stimuli were matched to the erotic ones regarding emotional valence and emotional arousal. More cogently, these results hint at specificity for the processing of erotic stimuli (Schupp et al., 2004b, 2006, 2007; van Lankveld & Smulders, 2008). This putatively specific response appears to depend on a match between erotic content and the subject's own sexual preference or orientation—a link that might even become apparent in subliminal perception of the erotic stimuli. Additionally, neuroelectric correlates of sexual arousal appear to be a useful research tool in refuting theories that base human behavior and decision mostly on rationality and logic.

A problem with these observed trends lies within the salient nature of sexual stimuli. Instead of the sexual content, the observed effects on the P3 and the LPP could alternatively be explained with stimulus salience, as erotic stimuli could also be seen as more salient compared to other emotional and

neutral stimuli. Both the P3 and the LPP have been shown to be influenced by the salience of a stimulus, and this process is also assumed to be mediated through attention (Dien, Spencer, & Donchin, 2004; Hajcak, MacNamara, & Olvet, 2010; MacNamara, Foti, & Hajcak, 2009; Olofsson, Nordin, Sequeira, & Polich, 2008). Future studies should try to replicate effects of sexual content on neuroelectric correlates while controlling for salient properties of sexual stimuli. Conceptually differentiating between sexual and salient properties of a stimulus might be a challenge as can be seen in studies where erotic stimuli have been used as experimental conditions of high motivational salience showing some conceptual overlap or synonymous use of the two aspects (e.g., Gard, Gard, Mehta, Kring, & Patrick, 2007). However, while sexual properties might make a stimulus most noticeable and salient, salience itself can be operationalized without the use of sexual content. Regarding alternative explanations based on differentiated stimulus properties, it should be noted again that both effects on the P3 and the LPP have been replicated with sexual pictures even when multiple other picture categories were controlled for emotional valence, arousal, physical properties (e.g., luminance), numerosity of objects depicted and also dimensions of approach and avoidance related to the pictures (Briggs & Martin, 2009; Feng et al., 2012; Uusberg et al., 2013b, 2014). It seems doubtful that further controlling using additional ratings on salience will undermine the effect of sexual content on the P3 and the LPP, but so far this has not been experimentally tested.

Another limitation in the present work could be seen in the treatment of faces as erotic stimuli. Both bodies and faces can be used to infer about physical attractiveness, and therefore, both stimuli were treated as erotic or sexual throughout this work. While both types of stimuli can be seen as highly salient and evolutionary important, faces could also be perceived as non-erotic stimuli. Pooling results from studies on faces and bodies could therefore result in an overestimation of the effect of sexual content on neuroelectric measures. Faces have a special place in the human brain (McKone, & Robins, 2011). They can immediately convey information about gender, race, age, etc., while at the same time humans can be regarded as experts when it comes to perceiving human faces. This special importance of faces could have confounded interpretations about the sexual content or the attractiveness of faces as a driving factor. However, it has been suggested that in cultures where normally clothes are worn a bias toward faces could at least partly reflect the learned fact that faces are regularly uncovered and therefore the quickest and most reliable cue for sexual and interpersonal information (Nummenmaa, Hietanen, Santtila, & Hyönä, 2012). Dissociated regions in the extrastriate cortex have been supported for the processing of bodies and faces (Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009), but when emotional information is perceived through faces and bodies both differences and

Table 6 Neuroelectric differences in abnormal sexual preferences

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Baker (1985)	–	38	Two groups [19 exhibitionists (mean age = 26.58, SD = 5.2) and 19 controls (mean age = 26.88, SD = 4.88)] perform 3 tasks	Resting state, verbal task and spatial task	qEEG	–	Increased frontal asymmetry (higher alpha activity left) in exhibitionists than in controls during rest. There was also a reduced (<i>n. sig.</i>) anterior–posterior intrahemispheric relation (left) in exhibitionists compared to controls
Batamirov et al. (1997)	–	129	Three groups [37 paraphiles, 43 with abnormal sexual behavior but without paraphilia, 49 controls (ages missing)] perform 3 tasks	Resting state, memorization test and mental arithmetic test	qEEG	–	Only individuals with paraphilia showed increased inter-hemispheric coherence in all ranges at posterior temporal and parietal sites. Increased level of asymmetric temporal desynchronization (theta) in the right hemisphere during visual–spatial task in groups with paraphilia compared to the other two groups The group was split into subgroups [17 paraphiles with gender identity distortions, 13 non-paraphiles with gender identity distortions, 49 controls (ages missing)] and results showed that paraphiles displayed lower beta 1 activity in the left hemisphere than non-paraphiles and higher interhemispheric coherence in alpha and theta in posterior temporal and parietal areas during resting Subsamples of 20 paraphiles with sadism (age missing), 17 paraphiles without sadism (age missing), 49 controls (ages missing) showed that paraphiles with sadism have an increase in hemispheric coherence in the temporal areas in theta, alpha and beta 1 during mental tasks

Table 6 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Berlin (1983)	–	2 (age missing)	Two pedophile case reports	Resting state	EEG (visual inspection)	–	Sharp activity over frontal regions, repeated slow waves (delta) and abnormalities (not specified) in the pedophile cases
Cassens et al. (1988) (abstract)	–	8 (age missing)	One group (paraphiles) performs multiple tasks	Resting state EEG and cognitive tasks	ERP, qEEG	Visual and auditory (not specified)	Decreased delta amplitudes and abnormalities (not specified) left frontal–temporal and right frontal
Corley et al. (1994)	–	24 (age and gender missing)	One group (sex offenders) performs one task	Resting state	qEEG	–	Decreased delta activity and coherence in posterior temporal sites (between left and right)
Emrich (1978)	4	32 (age missing [entire sample])	Three groups (sex offenders [$N = 23$, mean age = 38.7], sample was divided into 2 subgroups according to the viewing time for pictures of sexual delinquency [Deli-E: long viewing times, Deli-N: short viewing times] and compared to control group) perform task with 2 different picture categories	Rating task	ERP (visual inspection)	Pictures of sexual delinquency matched to individual offence of inmates with history of sexual crime	Deli-E: smaller N2 and larger P3 for sexual delinquency pictures than for scenery pictures Deli-N: higher N2 for sexual delinquency pictures than for scenery (only Deli-N group could be differentiated from control group using ERP)
Emrich (1979)	–	20 (age missing)	One group (sexual offenders) performs task with 2 different picture categories	Passive viewing	ERP (visual inspection)	Pictures of sexual delinquency matched to individual offences of inmates with a history of sexual crime	Some delinquents show higher amplitudes for pictures of delinquency than for neutral pictures and some delinquents show the reverse pattern

Table 6 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Flor-Henry (1987)	–	88	Two groups (31 exhibitionists and 57 controls [of comparable age = 33]) perform 3 tasks	Resting state, vocabulary exercise, word fluency exercise and block design exercise	qEEG	–	Reduced anteroposterior coherence in alpha during resting state and increased frontal-temporoparietal coherence (beta) in the right hemisphere during block design exercise in exhibitionists compared to controls
Flor-Henry et al. (1986) and Flor-Henry (1987)	–	58	Three groups (19 exhibitionists [matched to controls, mean age = 26.6, SD = 5.2], 20 exhibitionists [mean age = 29.1, SD = 8.2], 19 controls [mean age = 26.7, SD = 4.9]) perform 3 different tasks	Resting state, vocabulary exercise, word fluency exercise and block design exercise	qEEG	–	When exhibitionists (matched) were compared to controls, exhibitionists showed reduced bilateral anterior–posterior intrahemispheric relationships. During the rest condition, exhibitionist showed also increased posterior power. Frontal power was reduced in exhibitionists. These differences were found mostly in the theta and alpha band. Left intrahemispheric phase relations (anterior–posterior), left–right interhemispheric as well as right/left power ratios in alpha frequencies (during block design) differentiated the groups with highest probabilities
							When both exhibitionist groups were combined and compared to controls, exhibitionists showed differences mostly in alpha activity of frontal sites during block design exercise (less pronounced anteroposterior intrahemispheric relations (bilateral) and interhemispheric relations in the alpha range. Slower frontal alpha oscillation was also found and intrahemispheric anteroposterior relation (theta) was again reduced

Table 6 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Flor-Henry et al. (1988)	–	89	Two groups (43 exhibitionists [mean age = 29.1] and 46 controls [mean age = 33.7]) perform 3 tasks	Resting state, vocabulary exercise, word fluency exercise, and block design exercise	qEEG	–	Higher activity (alpha, theta, delta) in resting state and verbal processing tasks (left hemispheric) and reduced interhemispheric coherence in exhibitionists compared to controls (in vocabulary and word fluency task)
Flor-Henry et al. (1991)	–	98	Two groups (52 pedophiles [mean age = 33.1, SD = 9.2] and 46 controls [mean age = 33.7, SD = 8.6]) perform 3 tasks	Resting state, vocabulary exercise, word fluency exercise and block design exercise	qEEG	–	Higher frontal activity (alpha, theta, delta) and reduced interhemispheric and increased intrahemispheric coupling (both hemispheres) during word fluency tasks in pedophiles
Howard et al. (1994): Study 2	–	53	Two groups (34 child-sex offenders [19 heterosexuals (mean age = 39.2, age range = 22–59) and 15 with mixed orientations (mean age = 36.7, age range = 24–54)], control group of 19 heterosexual [mean age = 38.1, age range = 20–54]) perform task with 6 different picture categories	Picture matching task (S1 is compared to S2)	ERP (CNV)	Pictures of male adult, female adult, male pubescent, female pubescent (both 12 and 13 years old with visible secondary sexual characteristics), male child and female child (both 9 years old without visible secondary sexual characteristics)	No difference in CNV (vertex) between picture categories in sex offenders while the CNV (vertex) in the control group was influenced by age, gender and their interaction (of the stimuli) Further division of sex offenders into subsamples of 7 pedophiles and 8 non-pedophiles without further specification and comparison of the data: non-pedophiles show larger CNV (C3, vertex) to female adults than to female children while no such difference was observed in pedophiles

Table 6 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Ivashchenko et al. (1996)	–	88	Three groups (25 sexual offenders with paraphilia [mean age = 32.7, SD = 8.1], 23 sexual offenders without paraphilia [mean age = 28.6, SD = 7.1], 40 controls [mean age = 31.4, SD = 4.1]) perform 3 tasks	Resting state, memorization test and mental arithmetic test	qEEG	–	Higher general theta activity (occipital) and interhemispheric alpha coherence in paraphilia group compared to the other groups during resting with eyes open
Kirenskaya-Berus and Tkachenko (2003)	–	59	Three groups (19 controls, 19 patients with paraphilia, 21 patients without paraphilia [age missing]) perform 3 tasks	Resting state, memorization test and mental arithmetic test	qEEG	–	Patients with paraphilia showed increased interhemispheric coherence in posterotemporal sites and decreased interhemispheric coherence in frontocentral sites compared to the other groups. Patients with paraphilia also showed decreased spectral density in parietal central and orbitofrontal sites (in the right hemisphere) and increased interhemispheric asymmetry compared to the control groups. They also showed greater desynchronization and increases in beta (absolute spectral density and mean frequency) in frontal and central sites
Knott et al. (2016)	–	42	Two groups (22 pedophiles [mean age = 43.82, SD = 2.61], 20 heterosexuals [mean age = 41.55, SD = 2.75]) perform task with 4 different picture categories	Passive viewing (rating task after main task)	ERP	Erotic pictures (adults)	Larger early frontocentral potentials (P2, N4 at Fz) for erotic pictures than all the other stimuli were more pronounced in controls than in pedophiles

Table 6 (continued)

Study	Sample		Study design	Task	EEG	Sexual stimulation	Results
	Female	Male					
Waismann et al. (2003)	–	62	Two groups (28 paraphiles [average age = 35.6] and 34 heterosexuals [mean age = 28.8]) perform task with 3 different picture categories	Rating task	ERP (CNV)	Pictures with paraphile content	Paraphiles showed higher P600 to paraphilic pictures (F3, Fz, F4, C3, Cz) than controls

similarities have been described using fMRI (Kret, Pichon, Grèzes, & de Gelder, 2011). Using fMRI, it was also shown how sexual preference can influence the processing of faces with genders matching one's preference eliciting higher activation in face-specific brain regions and reward networks (Kranz & Ishai, 2006). Facial cues related to masculinity and femininity also influence attractiveness judgments as well as ERP (Carrito, Bem-Haja, Silva, Perrett, & Santos, 2018), and it has been suggested that sexual dimorphism in human faces has been shaped through sexual selection to advertise reproductive success (Puts, Jones, & DeBruine, 2012). Early studies have suggested that body attractiveness could have a higher impact on overall physical attractiveness, while the effect of facial beauty depends on body attractiveness (Alicke, Smith, & Klotz, 1986). Later approaches suggested also independent contributions to overall physical attractiveness (Peters et al., 2007) with an even more important role of facial attractiveness (Currie, & Little, 2009; Peters, Rhodes, & Simmons, 2007; Rau, Gong, & Zhuang, 2016).

When studies on faces were included in this review, they always contained comparisons of attractive and unattractive faces, operationalizing aspects of beauty and sexuality. Importantly, effects of attractive faces had similar pronounced effects on neuroelectric correlates like the use of other erotic stimuli when compared to non-erotic ones (Muñoz & Martín-Loeches, 2015). Accordingly, an argument can be made for the sexual value in attractive faces; however, future studies should explore how exactly sexual cues derived from bodies and faces map onto neuroelectric correlates. When bodies and faces are directly compared, they also show different effects on neuroelectric correlates (Muñoz & Martín-Loeches, 2015). Even if both body and face display cues for sexuality, they might not be redundant.

With regard to frontal alpha asymmetry, it should be noted that although in the studies reviewed here this measure was not researched as extensively as ERP, it has a high valence specificity compared to other measures. Inferring affective significance would be of central importance for the understanding of sexuality. As a measure, frontal alpha asymmetry indexes either less left than right frontal cortical activity or the reverse pattern (Reznik & Allen, 2018). This index has been linked to emotion regulation as well as psychopathology of affective disorders in many studies (van der Vinne, Vollebregt, van Putten, & Arns, 2017). It was assumed that left frontal regions are associated with affects of approach and appetitive motivation (Harmon-Jones, 2003), while right frontal regions are involved with inhibition and negative affect (Davidson & Irwin, 1999; Harmon-Jones & Allen, 1998). Within this approach-withdrawal model, e.g., a higher alpha activity in the right frontal hemisphere (reduced cortical activity) would imply a higher left-sided cortical activity and an approach motivation. Although some studies reviewed here somehow linked sexuality with frontal alpha asymmetry,

sometimes this was in line with the approach-withdrawal model (e.g., Schöne et al. 2016; Wacker et al. 2013) and sometimes it remains unclear on how to map the findings onto this model (e.g., Baker, 1985; Prause et al. 2014). Like studies with ERP, some inconsistent results might again be explained with a high methodological heterogeneity in the EEG recordings and calculations. New methodological recommendations on how to calculate the frontal alpha asymmetry should help clarify inconsistencies in the future and standardize methods (Smith, Reznik, Stewart, & Allen, 2017).

Gender Differences

While gender differences were not the focus of this work, some encountered studies should be discussed with respect to gender. When it comes to sexuality, gender differences have been researched on multiple occasions (Oliver & Hyde, 1993; Petersen & Hyde, 2010, 2011). Across a variety of sexual behaviors and attitudes no large gender differences were reported. Although men were more in favor of, for example, casual sex and the use of pornography, contrary to common knowledge gender differences in sexuality were generally small with within-gender variation being larger. However, these studies were based on self-reports and behavioral observations are also lacking in this field. Gender-specific reporting biases could have influenced results. Also, there have been instances where no different sexual arousals to picture content were reported between genders, but fMRI still showed different activations between the sexes with men having greater responses in the amygdala and the hypothalamus (Hamann, Herman, Nolan, & Wallen, 2004). Similar results were shown using ERP and focusing on emotions (Kemp, Silberstein, Armstrong, & Nathan, 2004). Another study using fMRI showed greater activation to female compared to male stimuli in men (e.g., inferior temporal lobe), but no such pattern was found for females when same-sex and opposite-sex pictures were compared (Rupp, Herman, Hamann, & Wallen, 2004). Later in a review it was mentioned that EEG data (CNV; Costell et al., 1972) supports this pattern (Rupp & Wallen, 2008) with men again differentiating more between same- and opposite-sex pictures. The studies reviewed in the present work rarely focused on gender differences and therefore were often not designed appropriately to test for gender effects. Still, the effect of stimulus gender on ERP was replicated again exclusively for men (Hietanen & Nummenmaa, 2011). When the picture content showed same-sex intercourse, however, only female participants showed differentiated LPC toward male sexual intercourse and female sexual intercourse (Yang et al., 2008). Significantly more pronounced LPP to erotic pictures as well as pictures of mutilations were also reported for male compared to female participants (Minnix et al., 2013). In an MEG study, naked bodies influenced an early component (mean latency of

126 ms) only in men while a later component (203 ms) was sensitive to naked bodies in both genders (Costa, Braun, & Birbaumer, 2003). In this study, men reported higher levels of arousal to opposite-sex nudes, while women did not differentiate between the stimulus gender. Interestingly, an early P1 (120–160 ms) component was sensitive to a 0.7 waist-to-hip ratio of animated bodies only in male participants (Del Zotto et al., 2017). This finding was discussed in support of the mate selection theory stating the importance of attractiveness in society and for reproductive success especially for women (Cornelissen, Hancock, Kiviniemi, George, & Tovée, 2009; Tovée, Maisey, Emery, & Cornelissen, 1999). Also, only in male participants did an early N1 (90–115 ms) correlate with subjective sexual arousal (Oliver et al., 2016). However, when EEG alpha power was calculated during a sexual film, the relationship between this measure and self-reported sexual arousal was stronger in female participants (Prause et al., 2014). More decreases in frontotemporal alpha (9.75–12.75 Hz) during erotic and sex films were also reported for women compared to men (Dimpfel et al., 2003).

When attractive faces were used, the effect of stimulus gender was also shown only for men (van Hooff et al., 2011). Although ERP data (N400) suggest that women and men process opposite-sex faces differently (Proverbio et al., 2010), male participants seem to differentiate more between attractive and unattractive faces (Zhang et al., 2016a) also when cartoon faces were used (Lu et al., 2014).

There were no gender differences regarding posture or position when erotic pictures were rated while EEG was recorded (Price et al., 2012) nor did gender influence the effect of tDCS on ratings of attractiveness (Ferrari et al., 2015). Further, no gender differences were found when pictures showed kissing with only partial nudity (Bartholow et al., 2010) or when a sexual insult (middle-finger jerk) was displayed (Flaisch et al., 2011). When the effect of repeated presentations of attractive faces was compared between genders, there was also no difference on the LPP (Thiruchselvam et al., 2016). Furthermore, when pictures of erotic couples and happy families were grouped together and presented in a flickering rate, no gender differences were found even though subjective ratings showed gender differences (Keil et al., 2003). As mentioned, ERP to auditory stimuli during erotic film seemed less suitable to investigate effects of erotic material. When such ERP were compared between genders, effects were also absent (Carvalho et al., 2011). Since studies were mostly not designed to investigate gender differences, some studies attribute the lack of findings in this regard specifically to inappropriate design or small sample sizes (e.g., Thiruchselvam et al., 2016; see also Alho et al., 2015 with a comparably small sample size).

In sum, neuroelectric correlates seem to show gender effects when attractive bodies (e.g., Hietanen & Nummenmaa, 2011) or faces (e.g., van Hooff et al., 2011) are shown

Table 7 Sexual seizures in epileptic patients

Study	Sample		Sexual behavior	EEG results
	Female	Male		
Amâncio et al. (1994)	–	1 (age = 31)	Orgasmic seizures	Isolated spikes in left temporal lobe during rest
Aull-Watschinger et al. (2008)	1 (age = 41)	2 (mean age = 43)	Orgasmic seizures	Non-lateralized theta activity, right ictal temporal spikes and ictal theta activity in right and left temporal area and sphenoidal electrode
Bachman & Rossel (1984)	–	1 (age = 55)	Orgasmic seizures	EEG shows no abnormalities during interictal phase
Ball (1968)	–	1 (age = 46)	Fetishism	No EEG abnormalities
Bancaud et al. (1970)	1 (age = 20)	–	Orgasmic seizures	Slow waves in right temporal lobe during rest, interictal diffused flattening and slow spikes during postictal phase in right temporal lobe
Bente and Kluge (1953)	1 (age = 44)	–	Sexual arousal	Low voltages, discontinuous alpha waves (all sites), low amplitude alpha waves with 10 Hz, precentral and frontal fluctuations (6 Hz) and 4 Hz waves in the left temporal lobe with one negative spike. Focal findings with slow waves in the left temporal lobe
Berthier et al. (1987)	–	1 (age = 43)	Seizures induced by orgasm	No EEG abnormalities during interictal phase
Bhaskaran (1955)	–	2 (mean age = 32)	Impotence	Maximal discharges in left frontal and parietal areas (case 1) and alpha spiking in left temporal area (case 2) during rest
Blumer (1969)	–	3 (mean age = 43.66)	Expressions of the opposite gender	Right-hemispheric slow activity (age related) and maximum slowing in temporal region) and mild voltage depression during resting state in only one of three cases
Blumer (1970)	8	42 (mean age [entire sample] = 35.3, age range [entire sample] = 17–65)	Hyposexuality, hypersexuality	Spike focus in anterior temporal lobe during resting state
Blumer and Walker (1967)	4	17 (age range [entire sample] = 17–47)	Hyposexuality	Reduced temporal spike activity after temporal lobectomy (and increase in sexual activity)
Calleja et al. (1988)	1 (age = 41)	–	Orgasmic seizures	Left central parietal focus while falling asleep and sharp waves in left central regions (C3-Cz), spikes in left central parietal sites during sleep
Chuang et al. (2004)	1 (age = 41)	–	Orgasmic seizures	Spikes in right temporal area during interictal phase

Table 7 (continued)

Study	Sample		Sexual behavior	EEG results
	Female	Male		
Crevenna et al. (2000)	1 (age = 37)	–	Orgasmic seizures	Sharp-wave focus in right temporal lobe (lasting 5 s)
Currier et al. (1971)	2 (age = 44.5)	–	Genital automatism and sexual verbalization, mild sexual aggression	Slow waves and focal spikes in left anterior temporal lobe during rest and drowsiness
Davies and Morgenstern (1960)	–	3 (mean age = 20.66)	Expressions of the opposite gender	Abnormalities and spikes in the temporal lobe during rest
Dobesberger et al. (2004)	6 (mean age = 37.33)	17 (mean age = 44.47)	Genital automatism	At seizure onset mostly bitemporal slowing and in some cases unilateral slowing in temporal sites
Epstein (1961)	–	4 (mean age = 36)	Expressions of the opposite gender and fetishism	Left and right temporal spike focus (occasionally only after Metrazol and Chloralose administration)
Epstein and Ervin (1956)	1 (age = 35)	–	Sexual repulsion	Right anterior temporal spike focus during onset of drowsiness and sleep and spikes and theta activity after 250 mg Chloralose-scopolamine
Ervin et al. (1955)	1 (age = 21)	–	Exhibitionism and bizarrely seductive behavior	Spike foci unilateral or bilateral temporal
Falconer et al. (1955)	1 (age = 22)	2 (age = 23.5)	Hyposexuality, exhibitionism	Spike or sharp-wave focus was in temporal regions and spike focus in the left anterior temporal region during resting state (on scalp and intracranial)
Freemon and Nevis (1969)	1 (age = 38)	–	Genital automatism and sexual verbalization	Slow (4–5 per second) and sharp waves in right temporoparietal area during rest
Gastaut and Collomb (1954)	8 (mean age = 40.37)	17 (mean age = 36.17)	Hyposexuality, impotence, hypersexuality, genital sensation, genital automatism, exhibitionism, sexual aggression	Foci in left, right and bilateral temporal regions
Gautier-Smith (1980)	3 (mean age = 23.66)	1 (age = 27)	Orgasmic seizures, exhibitionism	Right frontotemporal slow waves and left and right temporal discharges
Geier et al. (1975)	–	1 (age = 38)	Genital automatism	Spike and slow waves in right frontoparietal regions during rest, clear right frontal focus during psychomotor seizure and frontal discharge during seizure (intracranial)

Table 7 (continued)

Study	Sample		Sexual behavior	EEG results
	Female	Male		
Geier et al. (1976)	–	1 (age = 18)	Genital automatism	Waves of low rhythmic in right parasagittal lobe (scalp) corresponding with phasic slowing-down of rapid discharge in depth electrodes (during movement, intracranial)
Grabowska-Grzyb et al. (2006)	–	2 (mean age = 52.5)	Hypersexuality	Sharp and theta waves in left parietal region (interictal)
Hierons and Saunders (1966)	–	15 (age = 31–48)	Impotence	Spikes in anterior temporal lobe in left sphenoidal electrodes and spike focus in right sphenoidal electrode during rest
Hoinig and Duggan (1974)	–	1 (age = 17)	Expressions of the opposite gender	EEG abnormalities during resting state (not specified)
Hoinig and Hamilton (1960)	1 (age = 32)	–	Seizures induced by orgasm	Slow waves in right frontotemporal areas (5–6 cycles per second) before orgasm induced by hypnosis
Hoinig and Kenna (1979)	11 (mean age = 28)	35 (mean age = 30)	Transsexualism	Focal abnormal asymmetries and delta waves mostly in temporal regions (once in occipital regions) during resting state
Hooshmand and Brawley (1969)	1 (age = 32)	1 (age = 29)	Exhibitionism	Male patient: sharp waves and spikes in left temporal region during rest and more frequent during drowsiness and light sleep Female patient: after removal of tumor in frontal and anterior temporal lobe slow delta waves and spikes were recorded near that area (reduced seizure and exhibitionism)
Hosseini et al. (2013)	–	1 (age = 21)	Sexual aggression	Disturbances in the right temporal lobe
Hunter et al. (1963)	–	1 (age = 39)	Expressions of the opposite gender and fetishism	Spike focus in left anterior temporal lobe in sphenoidal electrodes during rest and underlying slow and theta activity in scalp sites (left temporal lobectomy relieved seizures and sexual tendencies)
Jacome et al. (1980)	–	1 (age = 26)	Sexual seizure	Spike discharges in right temporal lobe during interictal phases and bilateral slow-wave activity during ictal phase

Table 7 (continued)

Study	Sample		Sexual behavior	EEG results
	Female	Male		
Janszky et al. (2002)	1 (age = 31)	–	Orgasmic seizures	Seizure onset in right mesiotemporal lobe and independent spikes bitemporal (mostly right, intracranial)
Janszky et al. (2004)	5 (mean age = 48)	2 (mean age = 47)	Orgasmic seizures	Ictal and interictal right temporal and bitemporal spike activity (1 case with left activity)
Johnson (1965)	–	1 (age = 36)	Impotence	Irregular slow-wave activity in right frontal and posterior temporal sites during resting
Kennedy (1959)	1 (age = 24)	–	Orgasmic seizures, genital sensation	Spikes at the vertex
Kolářský et al. (1967)	–	86 (mean age = 26, age range = 15–43)	Voyeurism, exhibitionism, heterosexual and homosexual pedophilia, sadism and masochism, fetishism and expressions of the opposite gender, hyposexuality (in $N = 19$)	Focus in temporal lobe during rest
Leutmezer et al. (1999)	2 (age = 30)	3 (mean age = 36)	Genital Automatism	Regional rhythmic theta activity over left and right temporal lobe (ictal) and interictal bitemporal spikes
Mitchell et al. (1954)	–	1 (age = 38)	Fetishism, tendency for voyeurism	Before lobectomy: Intertictal spike focus on the left (basal electrode) and ictal frequent firing in the left frontotemporal (sphenoidal electrode) region a minute later after confronted with object of fetishistic preference resulting in clinical fit 30–40 s later. High-voltage slow activity frontotemporal After lobectomy: Described as normal with only occasional spike activity in the left temporal cortex in proximity to operation site and no change when exposed to object of fetishistic preference
Money and Hosta (1967)	–	1 (age = 6)	Sexual precocity	Seizure discharges during wake state and epileptic patterns during sleep (not specified)
Mulder et al. (1954)	2 (1 male [age = 43], 1 with age and gender missing)	–	Orgasmic seizures, genital sensation	“Diffuse abnormalities” (p. 488) not specified during resting state and slow waves with focus in left temporal lobe

Table 7 (continued)

Study	Sample		Sexual behavior	EEG results
	Female	Male		
Ozkara et al. (2006)	6 (mean age = 33)	–	Seizures induced by orgasm	Paroxysms and polyspike waves, bilateral sharp activity (more prominent on the right side), irregular spike and wave activity (predominantly left), epileptogenic zone on the right temporal side, epileptiform activity on the right anterior temporal side
Patarnello (1963)	1 (age = 24)	–	Orgasmic seizures	Bitemporal abnormalities (predominantly left)
Petrizter and Foster (1955)	–	1 (age = 14)	Exhibitionism, voyeurism, expressions of the opposite gender	Spike and high-voltage potentials and beta and delta rhythms predominantly in right hemisphere (but also in other sites) during resting state
Pond and Bidwell (1954)	–	1 (age = 13)	“Sexually perverse” (not specified, p. 1523)	Frequent firing in the left inferior temporal lobe during resting state
Reading and Will (1997)	1 (age = 44)	–	Orgasmic seizures	Epileptic focus in right anterior frontotemporal region
Rémillard et al. (1983)	12 (mean age = 37)	–	Genital sensation, orgasmic seizures and sexual seizures	Sharp wave and spike discharges in right, left and bitemporal epileptic focus during rest (only in 10 cases)
Ruff (1980)	1 (age = 43)	1 (age = 36)	Orgasmic seizures	Paroxysmal and spike activity in right parietal lobe (1 patient with glioma localized in right postcentral gyrus and 1 patient with a meningioma in falx pressing at the superior postcentral gyrus) during episode
Sengupta et al. (2010)	–	1 (age = 34)	Seizures induced by orgasm	2–2.5 Hz rhythmic delta in left temporal lobe spreading to right hemisphere during ictal phase
Shukla et al. (1979)	14	30 (mean age [entire sample] = 20)	Hyposexuality	Spike and slow waves over bilateral temporal areas during rest
Spencer et al. (1983)	1 (age = 14)	3 (mean age = 20)	Exhibitionism, genital automatism, sexual verbalization	Sharp-wave activity and right temporal slowing with right and frontotemporal spike focus during rest
Stoffels et al. (1980)	1	14 (age range [entire sample] = 11–42, mean = 23)	Genital automatism, orgasmic seizures	Left, right and bitemporal abnormalities as well as discharges in paracentral lobe and anterior cinguli

Table 7 (continued)

Study	Sample		Sexual behavior	EEG results
	Female	Male		
Surbeck et al. (2013)	1 (age = 49)	–	Orgasmic seizures	Induced orgasm by clinician was followed by discharge (18 s) in temporal pole, anterior–inferior insula, parahippocampal gyrus and left hippocampus
Tamuri et al. (2000)	1 (age = 48)	–	Orgasmic seizures	Bilateral irritative activity on temporal regions and spikes on the left temporal region
Terzian and Frugoni (1958)	1 (age = 50)	–	Orgasmic seizures, genital sensation	Resting state EEG hinted toward abnormalities in the centroparietal and right parasagittal areas where a tumor was later removed
Terzian and Ore (1955)	–	1 (age = 19)	Exhibitionism, hypersexuality	Epileptogenic focus in left temporal region during resting state
Torelli and Bosna (1958)	1 (age = 31)	–	Hypersexuality	Abnormalities in right posterior temporal lobe
Trevisol-Bittencourt and Troiano (2000)	–	1 (age = 35)	Hyposexuality	Irritative focus in right temporal lobe during rest
van Reeth et al. (1958)	2 (mean age = 43)	2 (mean age = 54)	Hypersexuality, orgasmic seizures	Right temporal abnormalities
Walker (1972)	–	1 (age = 16)	Orgasmic seizures, sexual aggression	Left temporal spiking during resting state
Williamson et al. (1985)	–	6 (age and gender missing)	Genital automatism	Medial and orbital frontal paroxysmal foci with high-frequency activity (intracranial recordings), bilateral interictal foci in temporal areas (scalp recordings)
York et al. (1979)	–	1 (age = 9)	Genital pain	Polymorphic 4–7-per-second wave forms in both hemispheres followed by rhythmic low-voltage 12-to 13-cycles per second in the right and central areas during and shortly after pain

Table 8 Sexual behavior during sleepwalking

Study	Sample		Sexual behavior	EEG results
	Female	Male		
Béjot et al. (2010)	2 (mean age = 38)	–	Sexual assault and sexual verbalizations	Complex partial seizures were absent during resting state but sudden arousals from slow-wave sleep
Cicolin et al. (2011)	1 (age = 61)	1 (age = 41)	Genital touching, masturbation, sexual assault	Sudden transitions from slow-wave sleep to wake state, hypersynchronous delta pattern before episodes as well as rapid alpha rhythms and persistence of delta activity during episodes
Ebrahim (2006)	–	1 (age = 22)	Rape	Hypersynchronous high-voltage delta waves arousal and delta wave cluster as well as spontaneous arousals from slow-wave sleep (induced by alcohol challenge) during sleep
Guillemineault et al. (2002)	4 (mean age = 26.75)	7 (mean age = 24.85)	Rape, masturbation, sexual assault, sexual vocalization	Short arousals, hypersynchronous delta during slow-wave sleep, sharp transients (Fp3-T3) as well as left mesiofrontal spike focus
Pelin and Yazla (2012)	–	1 (age = 31)	Masturbation	Anterior temporal and temporal regions show hypersynchronous delta waves (2–3 Hz, but also muscle artifacts) during masturbation and neuronal hyperexcitability was observed in right temporal cortex during masturbation under sleep
Shapiro et al. (2003)	2 (mean age = 39)	9 (mean age = 31.55)	Masturbation, sexual assault, genital touching	Arousals from slow-wave sleep, redistributions of slow-wave sleep patterns, alpha activity in slow-wave sleep

without the combination of other content (e.g., kissing) and men show more pronounced reactions compared to women (Minnix et al., 2013). Facial attractiveness had a stronger effect on male ERP than on female ERP (Zhang et al., 2016a). Men show also typically earlier responses toward sexual content (e.g., nudity, Costa et al., 2003) and a higher sensitivity toward the opposite gender (Hietanen & Nummenmaa, 2011), unless same-sex intercourse is displayed (Yang et al., 2008). While self-reported sexual arousal was more closely related to early ERP components in males (Oliver et al., 2016), in females alpha frequencies calculated during continuous and longer-lasting erotic films (Prause et al., 2014) and later components (P3b [385–600 ms]; Oliver et al., 2016) seemed more indicative. This is in line with the reported close relationship between early components (EPN) and penile erection in men (Ponseti et al., 2009). While both genders display genital arousal to the opposite sex (Spape, Timmers, Yoon, Ponseti, & Chivers, 2014), it seems that this arousal could be based on more initial early cortical processes in men than in women. Genital arousal and self-reports on sexual arousal seem to be in higher agreement in males compared to females (Chivers, Seto, Lalumière, Laan, & Grimbos, 2010). Early, automatic, and fast cortical processes might therefore be linking genital and self-reported sexual arousal in men while less immediate and automatic cortical functions allow for some independence between genital and mental sexual arousal in women. From an evolutionary point of view, the necessity for penile erection to have intercourse could require a more straightforward link in the male brain, while aspects of decision making and choosiness could somewhat weaken this link in women (Chivers et al., 2010). However, as mentioned above modern studies connecting neuroelectric correlates and female genital arousal are still missing. Different mating strategies between men and woman as proposed by sexual strategy theory could also account for gender differences (Buss & Schmitt, 1993; Li, Bailey, Kenrick, & Linsenmeier, 2002; van Hoof et al., 2011). According to this theory, men would prioritize signs of fertility (e.g., attractiveness, youth) and women would prioritize status or ambition. This would explain the more pronounced EEG signals in males to attractiveness when bodies and faces are shown in combination with the opposite sex. However, the stimuli used throughout all studies show a lack of differentiation of visible traits that could be associated with status or reproductive success from a female viewpoint, e.g., physical fitness derived from muscle composition (Lassek & Gaulin, 2009; Lukaszewski, Simmons, Anderson, & Roney, 2016) or body height (Case & Paxson, 2008; Nettle, 2002). While in men most pronounced neuroelectric reactions for erotic pictures do not support a negativity bias, in women it seems that unpleasant emotional content leads to more pronounced neuroelectric reactions when compared to male participants even when there were no differences in the ratings (Kemp et al., 2004).

Neuroelectric Differences in Abnormal Sexual Preferences

Looking at abnormal sexual preference, a specificity in the processing of sexual content with regard to a match between preference and stimulus quality seems to hold as well. Although the majority of the few pertinent studies available in this domain tried to achieve a distinction between healthy participants and participants afflicted by disorders of sexual preference with measures of cerebral asymmetry, this approach has been discontinued in recent years. Asymmetries, specifically in the alpha range in frontal sites, are presently being considered as expressions of a general state of sexual motivation within a sexual context regardless of preference. Asymmetries are not regarded as a biomarker for the possibly abnormal nature of a sexual preference that could possibly be detected from resting state brain activity. Although studies differentiating homo— from heterosexual individuals (i.e., variants of normal sexual orientation) also pursued this approach, the relative number of studies in the field of deviance using such between-group methods is much higher (3% of the studies listed in Table 5 vs. 62.5% of the studies listed in Table 6). Imaging studies focusing on sexual preference have localized brain activities in regions that were mentioned here in studies using intracranial recording or stimulation (septal region, thalamus, hypothalamus, parahippocampus) (Poepl, Langguth, Rupprecht, Laird, & Eickhoff, 2016). However, these studies have also relied on sexual stimulation to activate those regions (Poepl et al., 2016). Still prevalent difficulties for studies in the area of sexual deviance, apart from the same problems concerning the ERP experiments mentioned above, are the accessibility of such samples.

Disturbances in Sexual Behavior

Regarding the case reports on sexual seizures summarized in this review, the procedural standards used in clinical routine often reduce the level of evidence for the classification of the EEG data recorded to summary labels such as “normal” or “abnormal.” This allows for a subjective judgment on behalf of the researcher and bypass computational, statistical methods. The often mentioned and unspecific spikes or paroxysmal activities can lead to overinterpretation of subcortical processes as well as diagnosis of non-epileptogenic events (Benbadis & Tatum, 2003). In addition, most of the case studies suggest multimorbidity, also including other organic brain disorders. Only a few of the later studies used MRI to rule out structural lesions (e.g., Ozkara et al., 2006). This makes it difficult to separate functional from organic components and to draw meaningful conclusions from the case studies reviewed without running the risk of being misled due to biological

confounds. Furthermore, some reported EEG abnormalities were only observed after medication (e.g., Epstein & Ervin, 1956; Monroe, 1959) or attributed to other factors such as age (e.g., Blumer, 1969). Also, multiple cases showed normal EEG (e.g., Ball, 1968; Berthier et al., 1987; Case 1: Grabowska-Grzyb et al., 2006), while some abnormal findings are not specified further (e.g., Case 5: Hoenig & Duggan, 1974; Hosseini et al., 2013). The relationship between such electrocortical descriptions and human sexual behavior is thus difficult to evaluate. Although the episodic nature in which these sexual manifestations occur could suggest a connection to the epileptic states of the patient, the clarity with which these two episodic events can be distinguished at the subject level varies immensely from case report to case report. Most importantly, it should be emphasized that such seizure-related sexual manifestations are not indicative of the person's general sexual behavior. It is difficult to estimate the value of localizing such EEG abnormalities on the scalp to derive assumptions about the neurobiology of human sexuality. Neuroelectric signals in the mentioned case reports serve mostly diagnostic purposes for epilepsy. Many highly different sexual behaviors observed in the cases mentioned have been attributed to EEG abnormalities in the same regions and vice versa, though more parietal involvement was mentioned with conditions where genitals played a role (e.g., genital sensations and automatisms) and the temporal lobe was the most often mentioned region in relation to all sexual seizures in epileptics. Although patients with sexual seizures frequently show abnormalities and spike focus in temporal and fronto-temporal scalp areas, underneath which limbic structures like the amygdala, the hippocampus, and the hypothalamus are situated, it is difficult to draw conclusions about the subcortical processes just from electrical scalp recordings. MEG (Duez et al., 2016) and source reconstruction with EEG (Lascano, Vulliemoz, Lantz, & Spinelli, 2012) have been recommended for epilepsy but have not been used in most cases of sexual seizures so far. However, intracranial recordings from these subcortical areas have also been linked to orgasms and sexual arousal in patients (Bancaud et al., 1970; Nager et al., 2011). Sexual hyperactivity has also been observed in the Klüver–Bucy syndrome (Klüver & Bucy, 1937). This hypersexuality was one among many symptoms (e.g., visual agnosia and changes of dietary habits) first observed in rhesus monkeys after medial and anterior temporal regions including the amygdala were resected (bilaterally). In the mostly male human cases of Klüver–Bucy syndrome after traumatic brain injury, this inappropriate hypersexuality was the most observed symptom (Clay et al., 2018). Again, the temporal cortex seemed to play a role in sexual function.

The parallels between orgasm and epilepsy have been mentioned in previous works (Komisaruk & Whipple, 2011; Safron, 2016). An abnormally high degree of synchronous widespread activation of neurons was assumed for epilepsy

and has also been shown (fMRI) for orgasms (Komisaruk & Whipple, 2011). Such synchronous activations could also be generated from rhythmical and voluntary genital stimulation. Cases where tooth brushing triggered an orgasm would support this notion since tooth brushing also involves rhythmic stimulation (Komisaruk & Whipple, 2011; Safron, 2016). Neural synchrony seems to play an important role in seizures and orgasms. Orgasm could be seen as a system with a high threshold, needing a widespread and synchronous activation to be triggered (Komisaruk & Whipple, 2011). Interestingly, the mesial wall where representations of the genitals were initially assumed was not involved in orgasm in a SPECT study (Tiihonen et al., 1994). A high threshold for sexual climax could have evolutionary benefits such as avoiding wrong mating partners (Safron, 2016).

Distinguishing nocturnal seizures from sleepwalking is also not always a well-defined process. There was not enough EEG data reported to draw more meaningful conclusions on the relation between specific sexual acts during episodes and specific EEG patterns. Systematic examinations with large samples and quantified EEG signals are missing. So far, EEG findings from case reports are often reported as normal or do not go beyond the findings of normal sleepwalking episodes. In contrast to sleepwalking without sexual content, *sexsomnia* episodes occur with constant sexual arousal and seem to involve much more violent and injurious acts with higher frequency (Rhati & Bhatia, 2011). In this context, neuroelectric signals with possible relation to human sexuality have partly gained relevance in legal proceedings when the legal responsibility for sexual assaults resulting from *sexsomnia* is at stake (Mahowald, Schenck, & Crammer-Bornemann, 2007). The focus in such proceedings lied more in giving support for or against the automatic or conscious nature of that behavior and less in neuroelectric signals as correlates for sexual tendencies. In some (and perhaps many) of these cases, the diagnosis of *sexsomnia* or EEG findings could have been used as legal strategies to misdirect in order to avoid culpability. Visualization capabilities of modern neuroscientific methods including qEEG should be used with caution in legal proceedings (Jones, Marois, Farah, & Greely, 2013).

In medicolegal respects, the clinical evaluation of patients with *sexsomnia* is considered to determine their legal responsibility wherein the degree of automaticity and unconsciousness of a criminal act needs to be established. Albeit categorically different, within intentional sexual assaults as expressions of abnormal preferences, forms of automatic and unconscious processes are also plausible. Janssen, Everaerd, Spiering, and Janssen (2000) have proposed an initial automatic appraisal stage when perceiving sexual stimuli. Regardless of sexual preference, if there is a match between preference and stimulation, this would be evaluated in the first processing stages. The high time resolution of ERP methods has not yet been used to investigate

Table 9 Neuroelectricity and changes in sexuality

Study	Sample		Manipulation	Results
	Female	Male		
Ferrari et al. (2015)	10	10 (mean age [entire sample] = 22.9, SD = 1.9)	Transcranial direct current stimulation	Stimulation (2 mA, 20 min) led to higher attractiveness ratings for facial stimuli (irrespective of gender) but did not influence ratings on other dimensions
Heath (1972) and Moan and Heath (1972)	–	1 (age = 24)	Intracranial electrical stimulation	Initial heterosexual-oriented sexual activity from a homosexual (intracranial recordings from septal sites) showed increase in delta waves, fast superimposed frequencies, spikes and slow-wave activities (resembling seizures) immediately prior and during orgasm (when engaging with a prostitute)
Korda et al. (2009)	1 (48)	–	Electroconvulsive therapy	Stimulation completely reduced symptoms of Persistent Genital Arousal Disorder with later relapse of symptoms
Kwon et al. (2011)	–	11 (mean age = 36.9, SD = 7.8)	Sertraline (50 mg)	Sertraline increased the high beta frequency in superior frontal gyri (both sides) and in the right medial frontal gyrus in patients with premature ejaculation
Lee et al. (2010)	–	11 (mean age = 25.9, SD = 1.22)	Sertraline (50 mg)	The differences in current source density between a music video and the erotic film were only present in the placebo group Sertraline induced an increase in high beta frequency in the left precentral gyrus, the inferior, middle and superior frontal gyri only during the erotic film
McMullen and Agarwal (2016)	1 (29)	–	Transcranial magnetic stimulation	Stimulation completely reduced symptoms of Persistent Genital Arousal Disorder
Moan and Heath (1972)	1 (age = 34)	–	Intracranial chemical stimulation	Increased amplitude spindling activity (12 cycles per second) in septal regions during elevation in mood and spike and slow-wave activity (with superimposed low-voltage fast-wave modulation) during orgasm
Prause et al. (2016)	5	15 (mean age [entire sample] = 34.6, SD = 10.9)	Transcranial magnetic stimulation	Alpha activity in anticipation and reception of sexual reward was reduced with iTBS as compared to cTBS, while there was no difference with monetary reward (neither during anticipation nor reception)
Tripathi et al. (2016)	–	1 (29)	Transcranial magnetic stimulation	Stimulation of the supplementary motor area led to improvement of hypersexual symptoms

Table 9 (continued)

Study	Sample		Manipulation	Results
	Female	Male		
Wacker et al. (2013)	–	181 (mean age = 23.9, age range = 20–35, SD = 3.0)	Sulpiride pill (200 mg)	While higher trait approach motivation was linked to higher frontal alpha asymmetry (higher right than left) in the placebo group the reverse association was found for the D2 blocker group (higher left than right) and these effects were only present when the female experimenter was attractive
Yero et al. (2006)	2 (mean age = 55)	–	Electroconvulsive therapy	Stimulation reduced symptoms of Persistent Genital Arousal Disorder

whether objects appealing to sexual preference are processed in an initial automatic fashion. Studies have already established the specificity with which erotic stimuli are processed apart from other emotional stimuli and how this specificity is dependent on a match between preference and stimulus. Tasks on visual attention with emotional distractors are a useful way to research automaticity of early and fast cognitive processes (Carretié, 2014). The contralateral delay activity (Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; Vogel & Machizawa, 2004), an ERP component assumed to represent visual attentional demands (Larocque, Lewis-Peacock, & Postle, 2014), might also be useful in such an investigation. Instructional requirements to fake a sexual orientation in combination with ERP recordings could help to investigate whether the specific nature with which sexual stimuli are perceived is automatic, whether the specificity is an analogue of the automaticity, or whether deliberate processes guide the appraisal of sexual content. Automatic attentional processes toward erotic stimuli matching one's preference would have a large impact in terms of developing diagnostic tools for abnormal sexual preferences with forensic relevance. Thus, ERPs or event-related qEEG may bridge the gap between basic research in neuroscience and applied utility. However, further challenges need to be considered in this regard.

So far neuroelectric signals have shown clinical utility in certain areas (e.g., surgical aspects in epilepsy: Noachtar & Rémi, 2009, dementia: Adamis, Sahu, & Treloar, 2005, disorders of consciousness: Mikolajewska & Mikolajewski, 2014; Szurhaj, Lamblin, Kaminska, & Sediri, 2015), but their value in psychiatry is reduced to excluding organic causes. Apart from searching for diagnostic biomarkers (e.g., ERPs and connectivities) of psychiatric disorders, there have also been attempts to derive objective criteria from neuroelectric signals that could guide treatment processes (e.g., DeBattista et al., 2011; Khodayari-Rostamabad, Reilly, Hasey, de Bruin, & MacCrimmon, 2013). Predicting treatment response or relapse after treatment discontinuation based on neuroelectric signals is far from perfect though. It remains also unclear how those objective criteria should be interpreted (e.g., Kuo & Tsai, 2010; Ulrich, 2013). Another problem is that such predictors derived from neuroelectric signals will ultimately not be compatible with modern classification systems since those only have limited predictive validity and only describe symptoms (Cuthbert & Insel, 2013). But the development of a nosology based solely on such neuroelectric predictors is also missing. Computational psychiatry (Friston, Stephan, Montague, & Dolan, 2014; Montague, Dolan, Friston, & Dayan, 2012) offers approaches to bypass problems like that, and it remains to be seen whether problems with sexual needs can be targeted with such interventions (Moutoussis, Story, & Dolan, 2015).

Neuroelectricity and Changes in Sexuality

The studies reviewed on intended influence on sexual behavior have implications on therapeutic methods for sexual problems. Neuroelectric correlates related to genital stimulation were influenced through TMS (Prause et al., 2016), subjective ratings of attractiveness were influenced by tDCS (Ferrari et al., 2015), and medication influenced neuroelectric reactions toward the presence of an attractive person (Wacker et al., 2013). The effect of TMS and ECT on hypersexuality and persistent genital arousal disorder seemed less clear (e.g., Korda et al., 2009). Overall, studies have shown how neuroelectric correlates of sexual arousal can be experimentally targeted and influenced. A sexual context (e.g., through visual images) is usually necessary for such an endeavor. Research has moved from highly controversial invasive conversion therapies targeting anatomical structures without sexual context toward noninvasive methods using sexual stimuli. Attention to such stimuli has been suggested as a target for therapeutic research (Barlow, 1986; Prause, 2007). From the studies reviewed here, the ones with the least invasive means provide a promising basis for future research. Both tDCS and TMS of the DLPFC should be researched with a focus on their influence on attention to sexually relevant stimuli. Such methods have been examined as noninvasive means to, for example, increase activity of the DLPFC in several psychiatric disorders, ultimately increasing inhibitory control over impulses (Kekic, Boysen, Campbell, & Schmidt, 2016). Studies have shown that patients with sexual preference disorders are willing to participate in scientific work focusing on treatment options if confidentiality is not at risk and there is no moral judgment (Beier et al., 2009; Cantor & McPhail 2016). Hence, tDCS could ameliorate inhibitory control in individuals with sexual preference disorders.

Conclusion

As shown, neuroelectric correlates of human sexuality have been researched extensively, so the lack of overarching reviews integrating findings and summarized recommendations for future work is surprising. The present review hopefully provides a first comprehensive overview over some key points within this interesting field. Somatosensory centers for the genitals have originally been localized using intracranial stimulations. While research still continues, early findings from such stimulations had already hinted toward a more complicated representation (compared to somatotopic continuity) with connections to sensory perception related to the autonomic system. Somatosensory pathways from the genitals to the brain have also been detected using electrocortical recordings, showing surprisingly fast and preattentive relationships between genital sensation and cognition in the male brain. The cortical regions involved in genital

physiology are, however, only part of a far larger network of brain regions that is associated with orgasm. The unique mental state during orgasm itself is characterized by a likewise uniquely synchronous and widespread electrical activity in the brain hinting at a high threshold for its initiation and rhythmic requirements. Throughout other stages of sexual arousal, hemispheric asymmetries in brain activation have been repeatedly suggested with a predominant change in the right hemisphere. The temporal details of the neuroelectric correlates reviewed further support a reflexive and fast attentional processing of erotic stimuli that could be guided by automatic mechanisms. Compared to other emotional states, sexual arousal appears to influence neuroelectric reactions in a very specific way and such signals consistently differentiate sexual arousal by taking on their most pronounced form. This allows for a very quick differentiation of sexually relevant aspects in the human brain. Such a pronounced processing of sexually relevant stimuli could be linked to the high threshold for orgasm. The uniqueness of human sexuality might be explained with its connections to emotion, reproductive success, genital physiology as well as intimacy. Neuroelectric correlates of sexual arousal might also be a very useful research tool to uncover if and how mental states map onto brain states.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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