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# Homosexual and heterosexual men present characteristic patterns of cortical synchronization in response to visual sexual stimuli

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**Original Article** 

Abstract	Resumen	Tabla de Contenido	
Since several cortical areas participate in the processing of sexual stimuli, this study characterized the electroencephalographic activity of prefrontal, temporal and parietal areas in men with different sexual orientation while observing erotic videos with homosexual (HOV) and heterosexual (HEV) content. The homosexual group presented lower absolute power of theta band in the right temporal cortex and higher right fronto-temporal correlation of beta band when observing the HOV. While the heterosexual group rated only the HEV as pleasant, also presented a higher left fronto-temporal correlation of beta band while watching the HEV, and a lower right fronto-parietal correlation of theta band during observation of the HOV. These results show a characteristic cortical functionality involved in the processing of sexually-relevant stimuli and its possible association with sexual orientation.	Hombres homosexuales y heterosexuales presentan patrones característicos de sincronización cortical en respuesta a estímulos visuales sexuales. Debido a que diferentes áreas corticales participan en el procesamiento de estímulos sexuales, este estudio caracterizó la actividad electroencefalográfica de áreas prefrontales, temporales y parietales en hombres con diferente orientación sexual mientras observaban videos con contenido homosexual (HOV) y heterosexual (HEV). El grupo homosexual presentó menor potencia absoluta de la banda theta en la corteza temporal derecha, y mayor correlación fronto-temporal de beta cuando observaron el HOV. Mientras, el grupo heterosexual puntuó solo como placentero el HEV, también presentó una mayor correlación fronto- temporal izquierda de beta cuando observó HEV, y una menor correlación frontoparietal derecha de la banda theta durante la observación del HOV. Estos resultados muestran una funcionalidad cortical involucrada en el procesamiento de estímulos sexualmente relevantes, y su posible asociación con la orientación sexual.	Introduction Materials and Methods Results Discussion References	56 58 59 61 63
Keywords: EEG, sexual orientation, visual sexual stimuli,	Palabras clave: EEG, orientación sexual, estímulo		

prefrontal cortex.

Palabras clave: EEG, orientación sexual, estímulo visual sexual, corteza prefrontal.

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Sexual orientation is one of the factors that determine the physiological responses to sexual stimulation (Hu et al., 2011), that is classified in three categories: heterosexual, homosexual and bisexual (American Psychological Association [APA], 2008). In this context, several studies using functional magnetic resonance imaging (fMRI) have described a different pattern of brain activation during exposure to stimuli with sexual content in men with different sexual preference, for example, Safron et al. (2007) evaluated the brain regions involved in sexual arousal in homosexual and

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heterosexual men. Pictures with erotic content were used (naked man, naked woman, male-male and female-female). In general, it was found that the heterosexuals reported a greater sexual activation before the stimuli of women, while homosexuals did so for the stimuli of men. This was associated with a different pattern of activation. In the case of heterosexuals showed greater activation of temporal, occipital, the orbitofrontal cortex and the ventral striatum when they observed the stimuli of women, but there was no activation in any brain area when viewing the stimuli of men. Homosexuals showed greater activation in the cortex left medial prefrontal and in subcortical regions such as the ventral striatum, the caudate nucleus, dentate nucleus, and cerebellum.

Paul et al. (2008) evaluated the brain response of young heterosexuals and homosexuals while they watched erotic videos with heterosexual and homosexual content. They found that the brain response of heterosexual men to heterosexual stimuli was comparable to that of homosexual men to homosexual stimuli. Both groups presented a brain activation pattern characteristic of sexual arousal when watching videos that thev corresponded to their sexual preference, with activation in the orbitofrontal cortex, parietal and temporal and predominant activation of the hypothalamus. In contrast, when they saw sexual stimuli opposite to their orientation, hypothalamic activation disappeared, although activation in the prefrontal and parietal cortices persisted.

On the other hand, Hu et al., (2008) with the objective of determined if the brain activation patterns in homosexual and heterosexual men differ during visually evoked sexual arousal, showed that the viewing of erotic movie clips that induced sexual arousal was associated, in both groups, with activation of the middle prefrontal gyrus, the bilateral temporal lobe and postcentral gyrus, thalamus, insula, vermis, left precuneus, occipital cortex, and cerebellum. Specifically in the homosexual men, the left angular gyrus was activated; the caudate nucleus left and the pale right; while heterosexual men do not showed activation in these regions. Heterosexual men showed activation in the bilateral lingual gyrus, right hippocampus, and parahippocampal gyrus right, which were not activated in homosexual men. In both groups, analysis of the region of interest revealed no correlation between the magnitude of the amygdala or thalamus activation and reported

level of sexual arousal.

Based on above results, it is clear that menheterosexuals and homosexuals have differences and similarities in areas of cortical activation before the stimuli that are relevant to them or incentives to generate Sexual Arousal (SA). The role of these areas will be discussed in more detail below.

The prefrontal cortex participates in the processing of erotic stimuli and SA; because of that, is implicated in maintaining representations of erotic stimuli in working memory and in preparing to emit a response under those conditions (León-Carrión et al., 2007). The parietal areas have been related to attention, the processing of sexual stimuli, and sensations in corporal areas (Baird et al., 2007). While the temporal areas are most often involved in regulating human sexual behavior (Lilly et al., 1983), also participates in modulating the emotional meaning of sexual stimuli (Brooks et al., 1998) and, therefore, regulates interconnected cognitive and emotional processes (Redouté et al., 2000).

Many studies concerning neural bases of sexual orientation have been conducted using imageology (Kim et al., 2011), a technique that offers a poor temporal resolution. Nevertheless, a non-invasive procedure with high temporal resolution recording is the of electroencephalographic activity (EEG: Niedermeyer & Lopes da Silva, 1993). The frequency spectrum of the EEG is divided in multiple bands: delta ( $\delta$ ), theta ( $\theta$ ), alpha1 ( $\alpha$ 1), alpha2 ( $\alpha$ 2), beta1 ( $\beta$ 1), beta2 ( $\beta$ 2) and gamma ( $\gamma$ ), which permits to calculate the absolute power (AP) in microvolts by each EEG band; and correlation (rEEG), which has been used in several studies to determine whether the EEG connectivity between brain regions changes in relation to specific states (Corsi-Cabrera et al., 1997).

It has been reported that homosexual and heterosexual men present differences in EEG activity during verbal and spatial tasks (Alexander & Sufka, 1993). However, in the case of the EEG processing of visual sexual stimuli only one previous study has reported that homosexual men exhibited higher amplitudes in the theta and fast bands (alpha, beta and gamma) in the prefrontal cortex while observing a sexual video with heterosexual content compared to neutral content (Amezcua-Gutiérrez et al., 2021), however, in that study, the processing of homosexual stimuli by homosexual and heterosexual men was not considered.

Thus, the aims of present work were to: determine the valence and degree of general and sexual arousal, and determine the activity and degree of EEG correlation among the prefrontal, temporal and parietal cortices in homosexual and heterosexual men during observation of erotic stimuli with heterosexual and homosexual content. We hypothesized that the different perception and processing of such sexual visual stimuli will be associated with characteristic patterns of activity and functional connectivity among these cortices.

#### **Materials and Methods**

#### Subjects

Twenty-six healthy young men (20-35 years old), all right-handed. All participants had a minimum of 13 years of education and with a medium socioeconomic level as reported by the participants and according to the mean population income. They underwent a structured interview immediately prior to the study to determine their health status. All were overtly free of viral or bacterial illness, and reported no previous brain disease, psychopathology, or neural injury. Participants were recruited by personal invitation or over the Internet by e-mail or social media and invited to participate in a study voluntarily and without economic compensation, in which their brain electrical activity would be recorded while observing videos with explicit sexual interaction (both homosexual and heterosexual). The men were divided into two homogeneous groups according to their heterosexual or homosexual orientation, following the criteria defined below.

# Visual stimuli

Consisted of 5-minute fragments extracted from two videos in color without sound. The fragments of the heterosexual video (HEV) were taken from the movie Pirates (Joone, 2005) and consisted of scenes of explicit heterosexual intercourse between a light-skinned woman and a man. The video shows the action sequentially, from the moment they begin to undress and then caress and kiss each other, oral sex, until they reach penetration. The fragments of the homosexual video (HOV) were taken from the movie Major asshole (Scarborough, 2010), and show explicit homosexual intercourse between a pair of lightskinned men with the same sequential action as in the heterosexual video. To determine sexual orientation, subjects first answered the Kinsey scale (Kinsey et al., 1948), which ranges from 0 (for those who self-identify as exclusively heterosexual) to 6 (for those who selfidentify as exclusively homosexual), and 1-5 for people who recognize varying levels of desire for sexual activity with the two sexes, including "incidental" or "occasional" desires for sexual activity with the same sex. In this study, homosexual orientation included subjects that reported scores of 5 or 6, while heterosexual subjects were those with scores of 0 and 1.

In order to ascertain that participants did not suffer from any sexual dysfunction, each subject was also evaluated by the Arizona Sexual Experience scale (ASEX; McGahuey et al., 2000), a scale for men that quantifies sex drive, arousal, penile erection, ability to reach orgasm, and satisfaction from orgasm (corresponding to the week prior to the experiment).

To obtain a measure of the valence and degree of both general and sexual arousal induced by each video, immediately after each viewing, participants answered two scales during the 10-minute interval between conditions of the experimental session. The first was the Self-Assessment Manikin Scale (SAM; Bradley & Lang, 1994), a non-verbal pictorial assessment technique that directly measures pleasure (positive vs. negative valence) and general arousal (excited vs. relaxed). For valence, images that range from a smiling, happy figure to a frowning, unhappy one represents the pleasure dimension (stimuli rated from 1-3 were considered "unpleasant"; 4-6, "neutral"; and 7-9, "pleasant"). General arousal was rated on the basis of images showing an excited, wide-eyed figure to a relaxed, sleepy one. Here, ratings of 1-5 were considered "not activated", and 6-9 "activated". The second instrument was the Sexual Arousal Scale (SAS), which is based on the principles of the SAM Scale (a Likert-type scale) but was used to indicate the degree of subjective experience of penile erection (or sexual arousal) following observation of erotic stimuli. It consists of a series of five drawings of penises with different intensities of erection, where 1 = no erection (no SA) and 9 = very high erection(high SA; Hernández-González et al., 2013).

#### **EEG** recordings and procedure

All recordings were made in a soundattenuated room between 10:00 and 15:00 h. Electrodes were placed on the right and left frontodorsolateral (F3, F4), temporal (T3, T4) and parietal (P3, P4) cortices according to the 10-20 international system (Jasper, 1958), and referred to linked ears with impedances maintained below 10 Kohms. EEG data were recorded using a Nicolet EEG v32 System (Natus Neuro, Co., USA) with filters set at 1 and 60 Hz, and then digitalized at a sampling rate of 500 Hz and stored on a PC using CAPTUSEN software (Guevara et al., 2000).

In the testing room with the door closed, subjects were seated in a comfortable chair in front of a laptop and asked to place their right forearm on the table. They were instructed to relax and stay awake with eyes open during EEG recording. All EEG recordings were made in two conditions, each lasting five minutes, as follows: while watching the heterosexual (HEV) and while observing the homosexual video (HOV). The order of presentation of the two visual stimuli was counterbalanced. There was a 10-minute interval between conditions.

EEG signals were analyzed offline with CHECASEN software (Guevara et al., 2010), which displays the EEG epochs on the computer screen. By moving two cursors along the EEG signals it was possible to select and store artifact-free EEG segments (caused by eye movements, muscle activity, or heartbeat) that correspond to the specific periods of interest. For each participant, at least 30 epochs were selected from each video. Fast Fourier Transform analyses were applied in 1-s epoch samples, with the spectral graph ranging from 1-60 Hz at 1 Hz-resolution, that were performed using EEGmagic software (Guevara & Hernández-González, 2009). Absolute power (AP) was calculated for each condition and traditional EEG band: delta,  $\delta$  (1-3 Hz), theta,  $\theta$  (4-7 Hz), alpha1,  $\alpha$ 1 (8-10 Hz), alpha2, α2 (11-13 Hz), beta1, β1 (14-19 Hz), beta2, β2 (20-30 Hz), and gamma, y (31-50 Hz). Also, the correlation between cortices in the same hemisphere (intrahemispheric correlation, rTRA), and between homologous structures of both hemispheres (interhemispheric correlation, rTER) were calculated for each of the six frequency bands through of Pearson Product-moment correlation analysis. Correlation values were averaged over all epochs of the same condition for each participant and pair of derivations. To approximate a normal distribution, correlation values were transformed into Fisher's Z scores.

#### Statistical analyses

To determine the EEG differences between groups (heterosexual vs. homosexual) and

experimental conditions (HEV, HOV), a mixed 2x2 ANOVA (groups x condition) was performed with the AP, rTRA and rTER values from the frontal, temporal and parietal areas. Values with  $p \le .05$ were considered significant. Also, a post-hoc Tukey test was performed; as well as the effect size, we employed the eta square test. In the case that only the main effects were found, exploratory Tukey tests were also realized. In all cases that we made a Tukey test, we calculated the Cohen d-test to determine the effect size. For statistical purposes, AP values were transformed into logarithms (Gasser et al., 1982), while the correlation values were transformed to Fisher z scores. In the case of behavioral data, a Mann-Whitney U test for independent groups was applied to identify differences in the parameters of the Manikin and SAS tests.

#### **Ethical aspects**

The study was approved by the Ethical Committee from the Neuroscience Institute, University of Guadalajara, México (recording number: ET062017-249) and complied with all APA ethical standards and the 1964 Helsinki Declaration. Subjects were only allowed to participate after giving their informed consent. All participants were assured that confidentiality would be maintained and that they were free to withdraw from the experiment at any time without penalty.

# Results

The final sample consisted of 26 men who satisfied the inclusion criteria. Two groups were formed: one with heterosexual men (HEG, n = 13), the other with homosexual men (HOG, n = 13). HEG (mean age 25.46 years, SD = 1.98), HOG (mean age 24.69 years, SD = 2.75). On the ASEX test, both groups obtained scores within the normal range (11 and 13 respectively). No significant differences were found between them U = 63.50, p = .288.

# **Behavioral results**

HOG rated the HEV (Table 1) with lower valence scores than those reported by the HEG, U = 10.50; p < .001. No between-group differences were obtained for general arousal, and only a mild level of sexual arousal was induced by the HEV in both groups, but this did not reach the level of significance (Table 1). HOG rated the HOV with a higher valence U = 0.0; p < .001, higher general

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arousal U = 32, p < .007, and higher levels of sexual the HEV (Table 1). arousal U = 7.0; p < .001, than those reported for

#### Table 1.

Mean  $\pm$  2 standard errors of the scores on the SAM and SAS scales reported by the heterosexual (HEG) and homosexual (HOG) groups after observing the heterosexual or homosexual video.

	HETEROSEXUAL VIDEO		HOMOSEXUAL VIDEO					
	Valence	General arousal	Sexual arousal	Valence	General arousal	Sexual arousal		
HEG ( <i>n</i> = 13)	7.07 ± 0.61	5.84 ± 1.05	3.92 ± 1.07	2.84 ± 1.03	3.61 ± 1.21	1.46 ± 0.36		
HOG ( <i>n</i> = 13)	4.92 ± 0.53*	4.61 ± 1.02	$3.07 \pm 0.89$	7.00 ± 0.55*	6.23 ± 0.79*	5.30 ± 1.28*		

*Note*. \* $p \le 0.05$  HOG compared to HEG

# Electroencephalographic results Absolute power (AP)

No significant differences were found in the interaction of factors (groups x conditions), between groups, or between conditions in any of the EEG bands at F3, F4, T3, P3 and P4. In the case of T4, however, a main effect of factor B (conditions) was found for the theta band, with a small effect size  $F_B(1.24) = 5.62$ ; p = .025,  $\eta^2 = 0.01$ . The exploratory analysis revealed that only the HOG presented a lower AP of the theta band during observation of the HOV compared to the HEV, with a small effect size  $p \le .05$ , d = -.33 (Figure 1A, 1C).

# Interhemispheric correlation (rTER)

Regarding the degree of EEG coupling between hemispheres (i.e., the interhemispheric correlation, rTER), no significant differences were found in the interaction of factors (groups x conditions), between groups, or between conditions in any band (F3, F4, T3, T4, P3, P4).

#### Intrahemispheric correlation (rTRA)

With respect to the degree of EEG coupling between areas inside the same hemisphere (i.e., the intrahemispheric correlation, rTRA), no significant differences were found in the interaction of the factors (groups x conditions), between groups, or between conditions in any of the EEG bands.

It was only in the case of the rTRA between the derivations F4-T4 that a significant interaction of the factors (groups x conditions) for the beta2 band  $F_{AxB}(1, 24) = 4.18$ ; p = .049 was observed, with a small effect size ( $\eta^2 = .01$ ). The post hoc analysis revealed that the HOG presented a greater right

fronto-temporal correlation of the beta2 band during observation of the HOV than the HEV, with a small effect size (d = .39). No significant differences were found in the other bands (Figure 1B, 1C).

#### Figure 1.

EEG activity of the homosexual group during the observation of sexual stimuli



*Note.* Mean  $\pm 2$  standard errors of the different EEG bands of the homosexual group during observation of heterosexual (HEV) and homosexual videos (HOV); MD = Mean difference. A) Absolute power (in log) recorded in the right temporal cortex (T4). B) Intrahemispheric correlation (in *z*-values) between F4-T4. \**p*<.05 HOV with respect to HEV. C) Also, the schematic representation of all the EEG changes presented by homosexuals during observation of the HOV (as compared to HEV) is shown.

Regarding the F3-T3 rTRA, the beta1 and beta2 bands showed a significant interaction of the factors (groups x conditions)  $\beta$ 1:  $F_{AxB}(1, 24) = 6.04$ ; p = .016;  $\eta^2 = .02$  (small effect size).  $\beta$ 2:  $F_{AxB}(1, 24) = 4.25$ ; p = .048;  $\eta^2 = .01$  (small effect size). The post hoc analysis found that the HEG had a greater left

rINTRA of  $\beta$ 1 band (d = .15, small effect size), and a similar tendency of  $\beta$ 2 (d = .15, small effect size) while watching the HEV, compared to the HOV. No significant differences were found in the other bands (Figure 2A, 2C).

In the rTRA between F4-P4 a main effect of factor B (conditions) for the theta band was obtained, with a small effect size  $F_B(1, 24) = 5.33$ ; p = .026;  $\eta^2 = .01$ . The exploratory analysis showed that the HEG presented a higher correlation of the theta band in the right hemisphere while observing the HEV, compared to the HOV (d = .15, small effect size). No significant differences were found in the other EEG bands (Figure 2B, 2C).

#### Figure 2.

EEG activity of the heterosexual group during the observation of sexual stimuli



*Note.* Mean ± 2 standard errors of the intrahemispheric correlation (in Z-values) of the different EEG bands of the heterosexual group during observation of heterosexual (HEV) and homosexual videos (HOV); MD = Mean difference. A) Between left frontal and temporal cortices (F3-T3). B) Between right frontal and parietal cortices (F4-P4). \**p*<.05 HEV with respect to HOV. ° *p*<.08 HEV with respect to HOV. C) Also, the schematic representation of all the EEG changes presented by heterosexuals during observation of the HEV (as compared to HOV) is shown.

#### Discussion

This work confirms that sexual orientation is associated with a different preference to a visual sexually-explicit stimulus (Chivers et al., 2004; Hu et al., 2011). This different qualification of the erotic videos was related with a distinct cortical functionality in the participants, which could be related to different processing of each sexual stimulus.

Homosexuals were characterized by a lower AP of the theta band in the right temporal area as they watched the HOV. From a physiological perspective, the AP reflects the number of neurons that discharge synchronously; hence, it is an index of cortical information processing (Klimesch, 1999). Studies have described an association of the theta band to states of attention, as well as motivated and pleasurable states (Cervantes et al., 1992). The temporal cortex has been associated with the recognition of the emotions involved in visual stimulation (Brooks et al., 1998). In addition, a deactivation of temporal areas during perceived sexual activation and penile tumescence induced by erotic visual stimulation have been reported in young men by positron emission tomography (Redouté et al., 2000). It is also well-known that removal of the temporal lobes is followed by hypersexuality (Klüver& Bucy, 1939), which suggests that suppression of the possible tonic inhibition exerted by the temporal lobes allows the development of sexual arousal. Therefore, it is likely that the lower activation of the right temporal in the homosexuals could be associated with the disinhibition that allowed sexual arousal and/or the emotional processing (pleasant) that the homosexual subjects reported after observing the HOV.

When participants watched the video with erotic content of their sexual orientation, they presented a greater correlation between fronto-temporal zones in the beta bands. As mentioned above, EEG correlation is an index of functional connectivity between brain regions, where a high correlation indicates a similar functionality among regions (Guevara Pérez & Hernández-González, 2006). Therefore, our data show that when observing the stimulus of their orientation, both homosexual and heterosexual participants presented similar functionality between the prefrontal and temporal cortices, represented by a greater degree of coupling in the beta range.

The beta1 and beta2 bands have been related to the inter-neuronal communication of inhibitory networks (Whittington et al., 2000) and to the transfer of information between regions (Engel & Fries, 2010). The dorsolateral regions of the prefrontal cortex are related to goal-directed behaviors, to the evaluation and integration of emotional information, and to such executive functions as planning, working memory and inhibitory control (Mega & Cummings, 2001). Moreover, the temporal cortex has been related to sexual desire (Baird et al., 2007) and inhibitory processes implicated in sexual activation (Redouté et al., 2000). Therefore, the greater degree of coupling between prefrontal-temporal regions in the beta band during observation of the video of their orientation could be associated with analysis and integration of emotional information, which is prefrontal commanded by areas and the suppression of the inhibitory processes commanded by the temporal cortex. It may also be that this greater prefronto-temporal correlation in the beta band is associated with the inhibitory processes required to focus attention on erotic stimuli and, therefore, to generate a state of sexual activation according to the context.

This greater prefronto-temporal correlation associated with sexual activation induced by watching the erotic videos of their orientation shows a specific laterality in each group: in heterosexuals it appeared in the left hemisphere, while in homosexuals it was detected in the right hemisphere. Davidson et al. (1990), reported that pleasurable stimuli that induced an approach are associated with a greater power of the alpha band in frontal and temporal areas of the left hemisphere. Therefore. the areater prefronto-temporal correlation presented by HEG in the left hemisphere when observing the HEV is probably associated with the positive perception (pleasant, approach) and sexual activation induced by stimuli of their sexual orientation (heterosexual).

On the other hand, Fink et al. (1997) found a higher activation of the right hemisphere to stimuli that require more global visual processing. In this view, it is likely that the HOG will process the video of its orientation in a global way; unlike the HEG, which may require a greater focus on the specific aspects of the heterosexual stimulus (probably the woman in the video), as has been reported by Chivers et al. (2004; 2007). In this context, it has been proposed that the right hemisphere facilitates sexual arousal by not requiring complex analytical processing and by non-verbal processing information and sensations (Tucker & Dawson, 1984). Thus, it is likely that the greater right prefronto-temporal correlation observed in the HOG reflects the less analytical processing of the visual

stimuli as well as the greater level of subjective sexual arousal induced by the HOV.

Specifically in frontal and parietal regions, theta band has been related with selective attention (Başar et al., 1999). In light of this, it is likely that the higher right fronto-parietal correlation in the theta band observed in heterosexuals during observation of the HEV could support the fact that they process the sexual stimuli with greater selective attention (probably in the woman of the video). However, it is necessary to elucidate the cognitive aspects involved in the processing of sexual stimuli in order to corroborate this hypothesis.

In conclusion, sexual orientation is associated with the brain processing that young men assign to a visual stimulus with explicit sexual content (homosexual or heterosexual). The HOG showed a lower AP of the theta band in the right temporal cortex with greater right fronto-temporal correlation of the beta band while observing the HOV, which could be associated with the pleasant valence and the global or contextual processing of the stimulus with sexual connotation of their orientation. The HEG in contrast, presented greater left frontotemporal correlation of the beta band, and a higher right fronto-parietal correlation in response to the HEV, which could be associated with greater attention and cognitive processing focused on the specific aspects of the sexual stimuli.

#### Limitations of the study

This study is limited because we were unable to recruit a larger sample to, the difficulty to find men who fulfilled all the inclusion criteria. The sample comprised predominantly middle-class, welleducated men, factors that place some limitations on our ability to generalize findings. Although results of other studies have shown a direct correlation between self-reports of SA generated by visual sexual stimuli and objective measures of penile erection, it would be interesting to measure, by plethysmography, the exact degree of penile erection achieved while observing each video. Thus, further research designed to elucidate the cognitive and emotional processes involved in the processing of stimuli with sexual relevance in men with different sexual preferences, should be carried out.

# Availability of data, analytical methods and materials

The entire dataset, analytical methods and set of materials supporting the results of this study was published in the article itself, which are available upon request to the corresponding author.

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