Hearing what you see: distinct excitatory and disinhibitory mechanisms contribute to visually-evoked auditory sensations.

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Highlights

- Large ‘visual ear’ survey shows that many people ‘hear’ visual motion
- New genuineness test links objective to subjective measures of auditory sensations
- Visual surround disinhibition predicts stronger visually-evoked auditory sensations
- Excitability and inhibition each predict ‘visual ear’ and different trait clusters

Abstract

Visual motion or flashing lights can evoke auditory sensations in some people. This large-scale internet study aimed to validate a combined subjective/objective test of the genuineness of this putative form of synaesthesia (visually-evoked auditory response, vEAR). Correlations were measured between each individual's ratings of the vividness of auditory sensations evoked by a series of looping videos, and measurement of the videos' physical low-level motion energy, calculated using Adelson and Bergen's (1985) computational model of low-level visual motion processing. The strength of this association for each individual provided a test of how strongly subjective vEAR was driven by objective motion energy ('ME-sensitivity'). A second aim was to infer whether vEAR depends on cortical excitation and/or disinhibition of early visual and/or auditory brain areas. To achieve this, correlations were measured between the above vEAR measures and visual contrast surround-suppression, which is thought to index lateral inhibition in the early visual system. As predicted by a disinhibition account of vEAR, video ratings were overall higher in individuals showing weaker surround-suppression. Interestingly, surround-suppression and ME-sensitivity did not correlate. Additionally, both surround-suppression and ME-sensitivity each independently predicted different clusters of trait measures selected for their possible association with cortical excitability and/or disinhibition: Surround-suppression was associated with vEAR self-ratings and auditory-evoked visual phosphenes, while ME-sensitivity was independently associated with ratings of other traits including susceptibility to migraine and pattern glare. Altogether, these results suggest there are two independent mechanisms underlying vEAR and its associated traits, based putatively on cortical disinhibition versus excitability.

Introduction

For some people the sight of flashing shop displays, people walking, or any visual movement can evoke a phantom auditory sensation. This phenomenon was first described by Saenz & Koch (2008) in a small number of self-selected participants as a new form of synaesthesia. Our own recent investigations have uncovered more detail about this curious phenomenon, which we call the 'visually evoked auditory response' (vEAR or 'visual ear').Our findings to date suggest that vEAR may be substantially more prevalent (at least 20%) than canonical varieties of synaesthesia (e.g. 1-4%, Simner et al., 2006), and that it correlates with a broad range of perceptual traits, while the visually-evoked phantom sounds can interfere with detection of real faint auditory signals (Fassnidge, Cecconi Marcotti, & Freeman, 2017; Fassnidge & Freeman, 2018). We have previously proposed that vEAR may depend on individual differences in cortical excitability or disinhibition, and this is supported by our recent evidence of reduced competition between auditory and visual cortex (Fassnidge et al., 2019) as well as independent electrophysiological evidence of greater excitability in visual cortex (Rothen, Bartl, Franklin, & Ward, 2017). However, in contrast with other synaesthesias for which there are objective tests of genuineness (Simner et al., 2006), a similar objective measure of vEAR has so far been lacking. The present study sought to validate an objective test of vEAR based on the relationship between ratings of the auditory-vividness of videos, and a physical measure of the amount of raw 'motion energy' contained in the videos. Such a measure would help to identify individuals whose subjective reports can be reliably predicted given objective stimuli and measurements, compared to others who may experience such phenomena less strongly, or at least not as consistently. Taking precautions to avoid response biases, we then aimed to correlate the association of vEAR with other traits and perceptual measures associated with cortical excitability or disinhibition (Grossenbacher & Lovelace, 2001), including a psychophysical measure of visual surround suppression of apparent contrast (Xing & Heeger, 2001).

Objective tests of genuineness have been devised to establish whether subjective reports of canonical synaesthetic experiences relate to genuine sensory experiences (Eagleman, Kagan, Nelson, Sagaram, & Sarma, 2007). For example, in grapheme-colour synaesthesia such a test assesses the reliability with which an individual associates specific letters with specific colours, over repeated testing sessions, or whether speeded identification of a letter is implicitly aided or disrupted by displaying it in colours that are congruent versus incongruent with the individual's synaesthetic colour. Statistical regularities may exist between physical properties of a given inducer and its concurrent sensation (Bor, Rothen, Schwartzman, Clayton, & Seth, 2014; Witthoft, Winawer, & Eagleman, 2015), however it can be challenging to identify consistent psychophysical relationships between them. In contrast, the intensity of vEAR does seem to depend lawfully on the intensity of raw motion energy in the visual stimulus, as we established tentatively in an earlier study (Fassnidge & Freeman, 2018). We now seek further validation for an objective measure of vEAR genuineness based on this psychophysical relationship, which might provide insight into the underlying mechanisms.

In our previous study (Fassnidge & Freeman, 2018), participants were asked to rate the intensity of any auditory sensations evoked by live-action videos. We quantified the motion energy (ME) in each video using a simple model of spatiotemporal sensitivity of cells in early visual cortex to moving patterns (Adelson & Bergen, 1985), and used ME estimates to successfully predict intensity ratings for each video. When measured for each individual, the strength of this correlation between ME and ratings for each video can provide an objective and psychophysiological underpinning for subjective ratings of vEAR, which could serve as a measure of genuineness. A high correlation could indicate that vEAR is reliable and dependent on low-level mechanisms sensitive to visual motion; conversely low correlations might occur either if visually-evoked auditory sensations are very weak, and/or if they are more dependent on high-level scene interpretation rather than low-level characteristics of the visual imagery. For example, in the survey we previously used, some videos depicted collisions, bouncing, and vocalisation, and responses to these appeared to be strongly dominated by learned expectations of the associated sounds. Although some forms of vEAR may validly depend on such high-level semantic associations, in common with other forms of synaesthesia (Mattingley, Rich, Yelland, & Bradshaw, 2001; Myles, Dixon, Smilek, & Merikle, 2003; Smilek, Dixon, Cudahy, & Merikle, 2001), the present goal is to seek a purer measure of vEAR based on the psychophysical relationship between low-level visual motion and ratings of the intensity of auditory sensations. To avoid bias from high-level associations, the present study selected videos composed of computer-generated abstract motion rather than live action.

Studying vEAR may help to distinguish between different models of synaesthesia. The 'cross-activation' account of synaesthesia assumes that unusual patterns of cross-sensory associations are related to rare and idiosyncratic patterns of unusual neural connectivity (Bargary & Mitchell, 2008; Baron-Cohen, 1996; Hubbard & Ramachandran, 2005; Tomson et al., 2011). A contrasting 'disinhibition' hypothesis assumes that synaesthesia can result from disinhibition of feedback from higher areas to unimodal sensory areas (Grossenbacher & Lovelace, 2001; Neufeld et al., 2012), or more directly via disinhibition within the sensory areas themselves (Lalwani & Brang, 2019). In support of this latter hypothesis, our previous transcranial electrical stimulation study found physiological evidence of reduced competition between auditory and visual cortex (Fassnidge et al., 2019). There is further independent electrophysiological evidence of greater excitability in visual cortex in vEAR (Rothen et al., 2017). However, there has not yet been any test of an association between vEAR and other independent perceptual measures of inhibition.

The disinhibition hypothesis is tested here using the phenomenon of visual surround suppression, where the apparent contrast of a central test patch appears lower when surrounded by a similar high-contrast context (Chubb, Sperling, & Solomon, 1989; Xing & Heeger, 2001). This phenomenon is thought to depend on inhibitory gain control mechanisms in early visual cortex (Heeger, 1992). If vEAR depends on generally reduced cortical inhibition, this predicts that surround suppression should be reduced in vEAR. Interestingly, reduced surround suppression has already been found in patients diagnosed with schizophrenia, a condition typically characterised by auditory disturbances (Dakin, Carlin, & Hemsley, 2005); this in turn may be associated with a deficit in the inhibitory neurotransmitter γ-aminobutyric acid (GABA; Tibber et al., 2013; Yoon et al., 2009). However evidence for a role of GABA in synaesthesia is limited (Lalwani & Brang, 2019; Terhune, Song, Duta, & Kadosh, 2014)

The hypothesised role of systemic variables such as disinhibition has received further support from our previous finding that video ratings correlated with a variety of nominally unrelated perceptual traits (Fassnidge & Freeman, 2018), including the tendency to experience musical imagery, tinnitus, and also the little-known phenomenon of auditory-evoked visual phosphenes (Jacobs, Karpik, Bozian, & Gøthgen, 1981; Lessell & Cohen, 1979; Nair & Brang, 2019), which is an example of auditory-to-visual cross-talk. However, it is possible that some of these associations were subject to an acquiescence bias ('yea-saying'), where some participants might have tended to respond generally more positively than others to all questionnaire items. In an attempt to neutralise such a bias, the present study introduced a reverse-coded alternative for each trait question (see **Table 1**). It was randomly determined for each participant whether a given question had a positively or negative wording. The large sample size made it possible to directly compare average responses to the same question with wordings and thus assess any potential bias. The survey included a question about musicality, given our previous finding of higher vEAR prevalence in musicians (Fassnidge et al., 2019), and a question about the effects of background noise on speech comprehension, given its strong dependence on visual cues such as lipmovements (Ipser et al., 2017; Sumby & Pollack, 1954). The survey also probed futher traits that may be associated with sensory excitability or disinhibition, including susceptibility to migraine aura (Palmer, Chronicle, Rolan, & Mulleners, 2000; Tibber, Kelly, Jansari, Dakin, & Shepherd, 2014), pattern glare (Wilkins et al., 1984), insomnia (Van Der Werf et al., 2010) and photic sneezing (Langer, Beeli, & Jäncke, 2010).

Methods

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

Participants

The study protocol was approved by the Psychology Ethics committee at City, University of London. Participants were recruited anonymously via web-links appearing in popular media publications such as New Scientist (Firth, 2018) reporting on a previous publication about vEAR (Fassnidge & Freeman, 2018). Location data showed world-wide participation, concentrated mostly in UK, western and central Europe, north America, and parts of south America. Participants were not offered payment. Based on experience from our previous study, and the initially high numbers of individuals clicking through to the present survey, a target of about 9000 completing respondents was set. Of the 21201 participants who began the questionnaire, 9232 completed it (44%). Incomplete records were excluded from analysis. Of the completing participants, 5170 identified as female, and 3804 as male. Participants who selected age categories under 65 had a mean age of 34 years (SD 11); 152 other participants selected the 'over 65' category.

Materials and procedure

All materials and Matlab code for generating stimuli are available for download from Open Science Framework (Freeman, 2020), and may be used freely. No part of the study procedures was pre-registered prior to the research being conducted. The survey was administered using Qualtrics, in English, and can be accessed from tinyurl.com/vEARsurveyNS (see **Figure 1**). The survey contained sections probing a variety of traits, then eliciting ratings of video, and finally testing surround suppression.

The first section provided an explanation of the purpose of the study, *'An examination of the types of visual motion which evoke an internal auditory sensation'*, and information about anonymity and confidentiality. After informed consent, participants were prompted to identify their gender and select their age from following categories: 18-24, 25-34, 35-44, 45-54, 55-64, >65. The following introductory text and question about prior awareness of vEAR was then displayed:

‘We are interested in whether different types of visual motion evoke an imaginary sound, although in reality no such sound exists. The sound may be experienced within your head rather than in the outside environment. This may be perceived in a number of different ways. You may experience it as if you are vividly imagining the sound, or it may sound like a ringing in your ears, or it might resemble the experience of 'hearing' phrases of a popular song in your mind's ear, or the voices of people on television when watched with the volume off. Alternatively it may be an abstract experience, but closer to being an auditory experience than a visual experience. Some people describe it as imaginary white noise. To avoid confusion we will from now on refer to any such experience as ‘auditory sensation’ rather than hearing. What is important is that the auditory sensation occurs in time with visual change over time, caused by motion or sudden flashes. It is typically involuntary (i.e. it happens automatically rather than as a result of conscious effort) and it happens consistently.
Have you previously been aware of experiencing this type of auditory sensation when viewing visual movement? [Yes / No / Not sure]’

The next section included 11 compulsory questions about traits (**Table 1,** and see **Figure 1**a for an example display). Some items included brief introductory definitions and relevant weblinks, e.g. ‘*An earworm, sometimes known as Involuntary Musical Imagery, is a catchy piece of music that continually repeats through a person's mind after it is no longer playing. https://en.wikipedia.org/wiki/Earworm”.* Each question item had two alternative wordings (**Table 1**). One version was positively worded (e.g. *‘I suffer from tinnitus’*) and the other negatively (*‘I do not suffer from tinnitus’*), and participants were required to indicate their agreement with the statement on a scale from 0 (‘disagree strongly’) to 5 (‘agree strongly’). In addition, in some questions the absence of a trait was phrased positively (e.g. ‘*I can walk in bright sunshine without experiencing the urge to sneeze*’), and the presence was phrased negatively (e.g. ‘*I cannot walk in bright sunshine without...’).* One version of each pair was randomly allocated to each participant. These features were intended to neutralise any acquiescence bias towards generally agreeing with statements, and to counteract any potential biases from social-desirability and demand characteristics present in the statements. In analysis, responses were reverse-coded as appropriate so that a higher rating indicated the presence of a trait. All questions were compulsory, however for one question about experiencing aura with migraine a ‘not applicable’ option was included for participants who do not suffer migraine.

The video rating section contained 20 colour videos sequences (**Figure 1b**). Each was presented on its own webpage with a question and rating scale beneath. Video duration varied between 0.4 and 8 seconds, looping continuously until the participant responded to the question and clicked on to the next page. Image size was 495x495 pixels. Videos were selected with the criterion that they should contain motion across a range of velocities and accelerations, be graphically abstract and avoid depicting natural scenes, or events that might naturally be associated with sounds, such as collisions, frictions or explosions. Of these videos, 16 were downloaded royalty-free from giphy.com using the search term ‘abstract’. Two further videos were made depicting a grating undergoing periods of oscillatory motion at a range of frequencies. Two additional videos showed the much-publicised skipping-pylons sequence (credit: HappyToast), depicting heavy objects hitting the ground with camera-shake. These videos typically obtained high ratings but were not included in the analysis, which focused on abstract rather than live-action depictive imagery. Instructions at the beginning of the video section of the survey asked participants to *‘rate the clips from 0 (no auditory sensation at all) to 5 (very vivid and definite auditory sensation)’*. For each video participants were then asked *‘on a scale from 0 to 5, how much auditory sensation do you experience when watching this video?’*. Order of items was randomised for each participant.

The final section tested for surround suppression (**Figure 1c**). An initial page displayed a sample surround-suppression stimulus (described below) with instructions to adjust screen brightness until all patches were clearly visible. The stimulus set comprised 14 gray images, displayed in 8-bit colour depth, with dimensions 500x500 pixels (dimensions are given in pixels rather than visual angle because viewing distance could not be controlled). Gamma correction was applied using an exponent of 1/2.2 for a typical computer display. Each stimulus comprised a central ‘target’ disk of 30x30 pixels, in the centre of a circular ‘surround’ disk measuring 200x200 pixels, with no gap between them. The Michelson contrast of the target was always 30%, while the surround was displayed at 100% contrast. These stimuli comprised bandpass filtered noise centred on a wavelength of 6 pixels, and with a bandwidth of one octave. The filter was oriented at 45° or 135° ±20°, to give the appearance of an irregular grating. The central target orientation was either co-oriented or orthogonal to the orientation of the surround. Seven examples of each were tested, presented in random order. Each display also comprised five peripheral ‘sample’ disks, each with the same dimensions as the target patch. Each disk had a different contrast, selected from the following: 5%, 17.5%, 30%, 42.5%, 55%. These were arranged in random order around the main centre-surround display, in a circle with radius 180 pixels. Disks were labelled in clockwise order with the numbers ‘1’ to ‘5’. Coloured rings indicated the locations of the central target and peripheral samples, flashing briefly for 200ms every 5 seconds. Each of these 14 images were presented once on their own webpage, in random order for each participant, with no time limit for viewing. Instructions under each display asked participants ‘*Which of the peripheral disks has the same contrast as the central disk?’.* Although the term ‘contrast’ might not have been familiar to many respondents, the presence of a whole range of numbered disks, each differing most noticeably in their contrast, was considered likely to provide a good visual cue to what was the relevant dimension for matching with the central patch. Compulsory responses were entered using radio-buttons numbered 1 to 5, corresponding to numbers displayed next to each peripheral sample disk. Upon entering their response, participants clicked through to the next page until all 14 trials were completed.

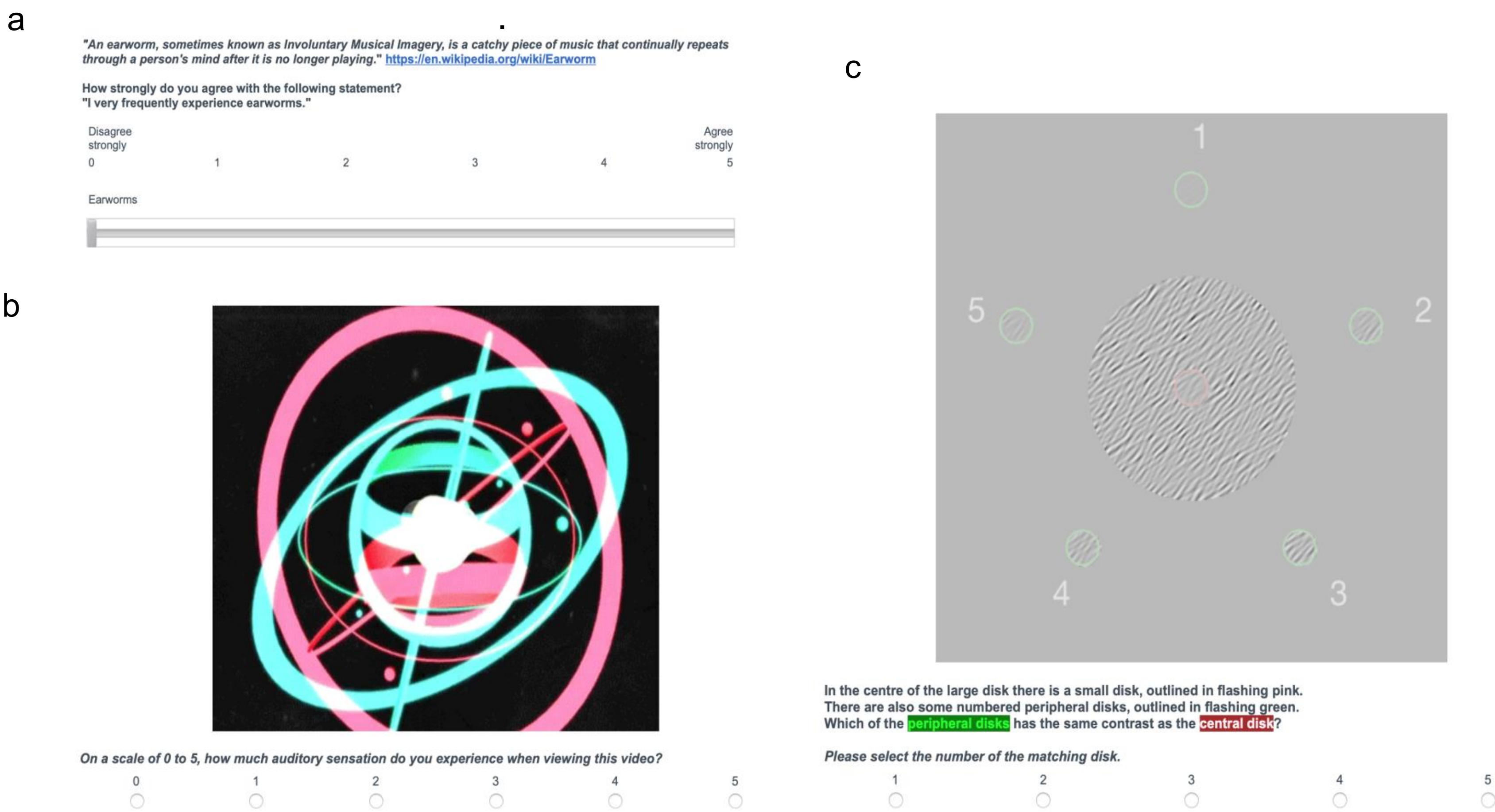

Figure 1 Examples items from vEAR survey: (a) trait question, (b) video rating, (c) surround suppression (with coloured placeholders which were only intermittently displayed).

Results

Raw data and Matlab code used to analyse the data are available for download from Open Science Framework (Freeman, 2020), and may be used freely. No part of the study analyses was pre-registered prior to the research being conducted. Analysis of the surround suppression data showed a significant effect of surround orientation on perceived contrast of the central test patch [$t(9231) = 92.83$, $p<0.001$, Cohen's D = 0.91]: co-oriented surrounds resulted in significantly lower matching contrast (Mean: 21.2% Michelson contrast, Standard Error 0.07%) compared to orthogonally-oriented surrounds (Mean: 27.32%, SE 0.068%). Surround suppression scores (SS) were derived for each individual by subtracting matching contrast for co-oriented surrounds from orthogonal. Positive SS values indicate greater suppression from co-oriented surrounds.

Internal consistency of video ratings was high [Cronbach's α= 0.96]. To derive a measure of individual sensitivity to Motion Energy, each individual's data were analysed in a linear regression, predicting ratings for each video from the motion energy of each video. The slope of the fitted model provided an individual measure of sensitivity to motion energy (ME-sensitivity). There was no significant correlation between SS and ME-sensitivity [$r(9230) = .01$, ns]. Histograms for each measure are shown in **Figure 2a to c,** showing smooth distributions.

When asked whether they had previously experienced phenomena that matched our written description of vEAR, 40% of participants answered 'Yes', 31% were 'Not Sure' and 29% answered 'No'. The proportion of 'Yes' responses was substantially higher than previously found (Fassnidge & Freeman, 2018), but this may be due to the publicity that vEAR has been continuing to receive. Responses to this question were used to group participants and compare measures of mean video ratings, SS and ME-sensitivity. Mean video rating were significantly higher in participants who responded 'Yes' to the question about Previous Awareness of vEAR compared to 'Not Sure' [t=19.63, Cohen's d=0.48, $p_{bonf}< .001$] or 'No' respondents [t=35.85, Cohen's d=0.90, $p_{bonf}< .001$; Kruskal-Wallace: $\chi^2(2,9229) = 1236$, $p<.0001$] (see **Figure 2d**). In a similar analysis, SS scores were significantly lower in 'Yes' respondents compared to 'Not Sure' [t=2.58, Cohen's d=0.069, $p_{bonf}< .01$] or 'No' respondents [t=3.60, Cohen's d=0.091, $p_{bonf}< .001$; $\chi^2(2,9229) = 11.77$, p=.003] (**Figure 2e**). Likewise, ME-sensitivity scores were significantly higher in 'Yes' respondents compared to 'Not Sure' [t=4.90, Cohen's d=0.117, $p_{bonf}< .001$] or 'No' respondents [t=13.25, Cohen's d=0.34, p_{bonf}< .001; $\chi^2(2,9229) = 237.19$, p<.0001] (**Figure 2f**).

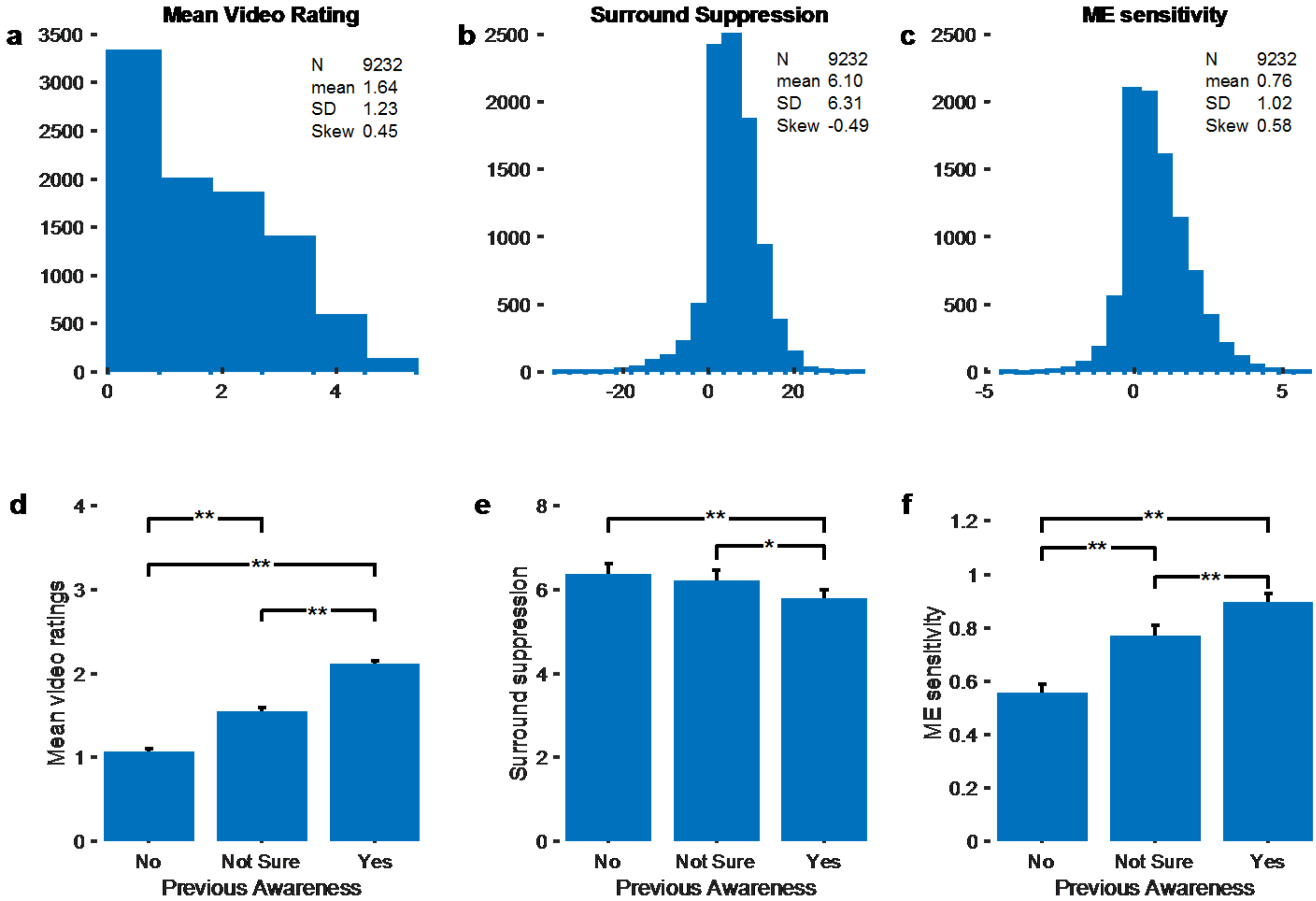

Figure 2 Histograms plotting the frequency of (a) Mean video ratings, (b) Surround suppression scores and (c) beta values for ME-sensitivity. Mean scores for (d) video ratings, (e) surround suppression and (f) ME-sensitivity, split by responses to a preliminary question about 'previous awareness' of vEAR. SE error bars; * p<.05; ** p<.01.

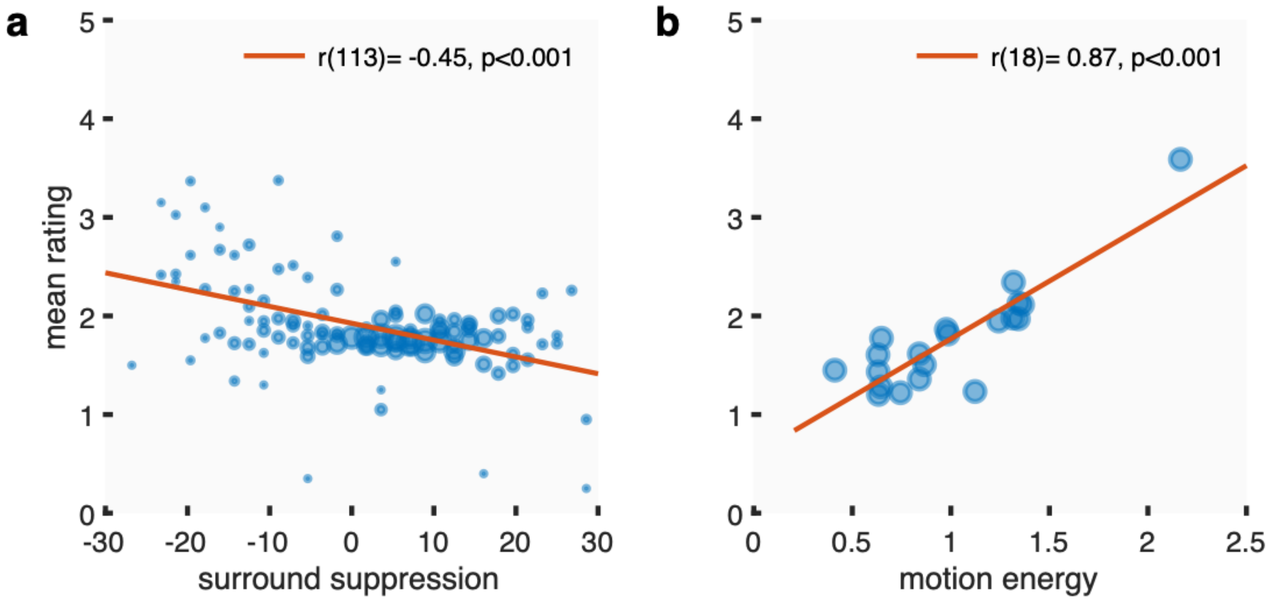

Figure 3 Scatterplots of (a) mean video ratings against surround suppression scores, where each dot represents an average video rating across a sample of participants who all had the same given value of surround suppression. The size of the dot represents the relative frequency of each of 115 unique combinations of surround suppression values and mean video ratings; (b) mean video rating against motion energy for different videos. Least-squared line of best fit is shown in red, with Pearson's correlations coefficients in the legend.

In a set of linear mixed effects analyses, models were compared with fixed variables predicting individual video ratings from each individuals' Surround Suppression score (SS), and/or each video's ME, and including subjects as a random variable. Three models were compared using a likelihood ratio test. Log-likelihood of a model including both SS and ME predictors was significantly higher than a model including ME only [$\chi^2(1) = 8.17$, $p = 0.004$]. Adding the interaction term (SS x ME) made no significant difference to the log-likelihood estimate compared to the purely additive model [$\chi^2(1) = 1.73$, ns]. The final model predicted 56.7% of the ratings variance with the following equation: Ratings = -0.0057*SS + 1.17*ME + ε [SS: $t = -2.86$, $p = 0.004$; ME: $t = 177.3$, $p < .0001$] (**Figure 3**). In summary, weaker surround suppression was associated with overall higher video ratings, but this effect worked additively rather than modulating the dependence of video ratings on motion energy.

All traits correlated significantly and positively with video ratings, regardless of whether the analysis included only positively-worded or negatively-worded questions [p<.003] (see **Figure 4** and **Table 2**). After Bonferroni correction, all correlations remained significant and positive [p<.05]. For some traits positively-worded questions yielded significantly stronger correlations than negatively-worded (**Table 2**). This might be explained if the negatively worded questions were harder for respondents to interpret. If acquiescence bias were the only factor underlying the correlation between video ratings and traits, this would have predicted negative correlations for the negatively-worded questions, which were reverse-coded, however all correlations were significantly positive. The following trait analyses combined data across positively-worded and negatively-worded versions.

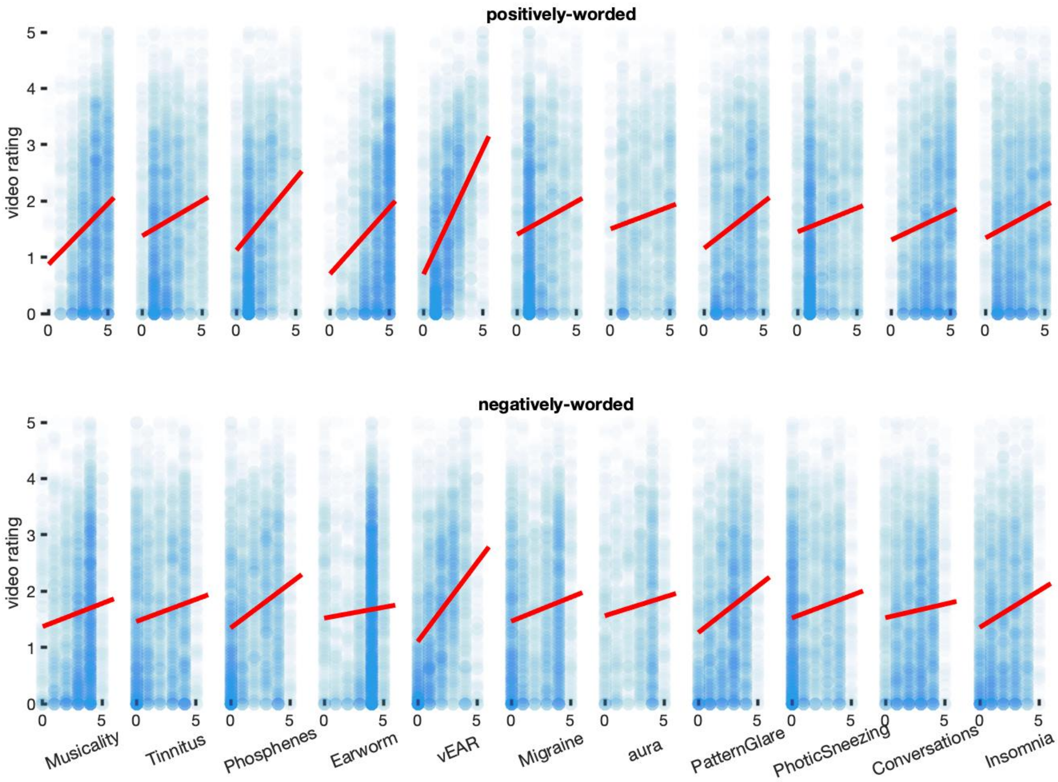

Figure 4 Scatterplots illustrating correlations between video ratings (horizontal axis) and ratings for different traits (vertical); separate rows of graphs for positively-worded versus negatively-worded trait questions. Colour saturation represents frequency of responses. Regression lines are superimposed.

A set of separate regression analyses next assessed whether ME-sensitivity and SS scores could predict each of the traits questions (**Table 3**). ME-sensitivity predicted all but two traits (‘photic sneezing’ and ‘speech-in-noise impairment’), all with slopes significantly greater than zero (p<.05, after Bonferroni correction, see yellow bars in **Figure 5a**). Weaker surround suppression independently predicted higher ratings for Musicality, Phosphenes, and vEAR, showing significantly negative slopes (**Figure 5b**). Although often highly significant, these predictors only accounted for a very small fraction of the overall variance in trait ratings (**Table 3**). Repeated analysis including an interaction term showed no significant interactions between ME-sensitivity and SS, and a negligible improvement in model fits (mean .02%, SE .007). As a complementary non-parametric analysis, Table 3 also reports Spearman’s partial correlations for each trait with either ME-sensitivity or SS, controlling for the other measure. The pattern of significant and non-significant associations is almost the same as for the regression analyses, with the exception of Phosphenes for SS.

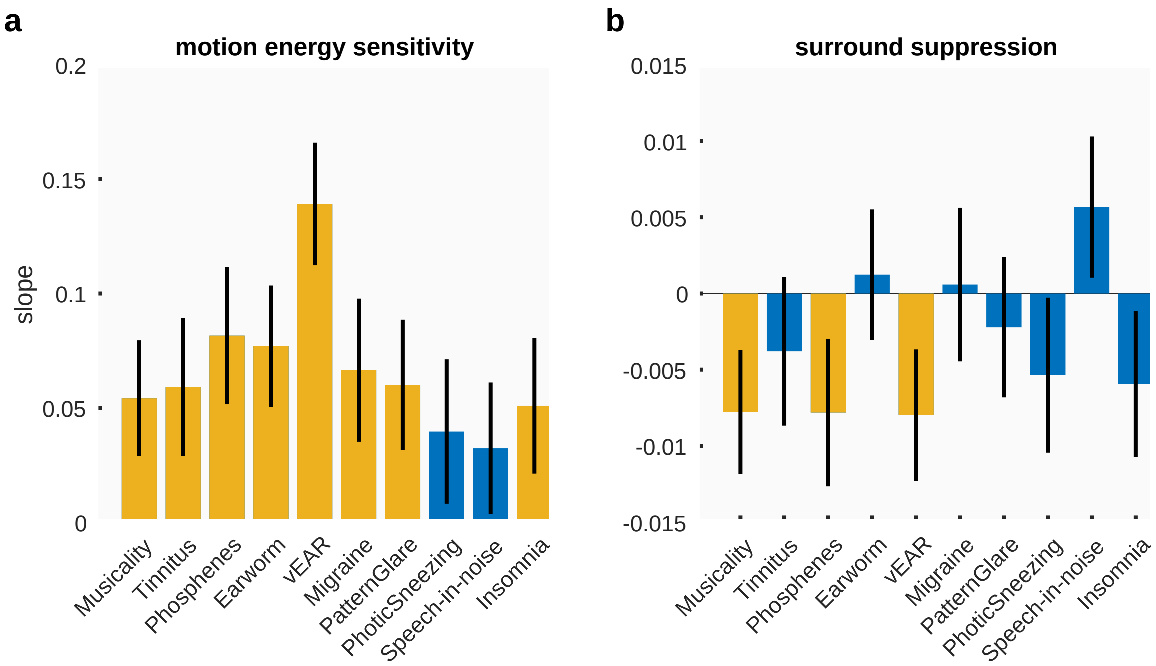

Figure 5 Results of linear regression analyses, predicting ratings for each trait from (a) ME-sensitivity scores and (b) surround suppression scores (i.e. Rating = ME + SS + ε). Bars in each graph show the slope relating each predictor score to the rating. Yellow bars indicate where slopes are significantly different from zero (p<.05, Bonferroni corrected). Errorbars show uncorrected 95% confidence intervals.

Discussion

This study has broadly achieved its initial goals: (1) an measure of vEAR genuineness has been validated, which allows us to identify individuals whose subjective ratings of the auditory vividness of silent abstract movies are reliably predicted by the objective low-level motion energy contained by the videos; (2) support has been obtained for the hypotheses that vEAR depends on increased cortical disinhibition, showing consistent associations between video ratings and the reduction of visual surround suppression in an independent psychophysical test. In addition to this, the detailed pattern of associations found between a broad set of perceptual traits and each of our two objective measures of motion energy sensitivity and surround suppression, suggests that excitatory and inhibitory mechanisms may independently govern the perceived intensity of vEAR. Altogether these results reveal the lawful psychophysical relationship between objective visual motion and subjective auditory sensation, and point to systemic neurophysiological variables that might account for vEAR along with a diverse variety of other associated perceptual traits.

The first finding is that average ratings of each video can be reliably predicted by the output of a popular model, in which visual motion in a stimulus is detected by filters which possess spatiotemporal filtering characteristics resembling cells found in early visual cortex (Adelson & Bergen, 1985). This goes further than our previous study (Fassnidge & Freeman, 2018) which used live-action videos, where ratings appeared to be heavily dominated by the availability of learned associations between the depicted visual events and what they are expected to sound like. The present results imply that vEAR need not depend on prior processing of high-level semantic features as do some other forms of synaesthesia such as grapheme-colour (Mattingley et al., 2001; Myles et al., 2003; Smilek et al., 2001), because auditory sensations can be evoked by raw abstract motion which has no meaningful association with any specific sounds. We can now understand vEAR in terms of normal low-level motion sensitive mechanisms, presumably originating in early visual cortex, which in some individuals may feed into auditory and/or multisensory areas via routes that do not necessarily involve semantic analysis.

While the motion energy model predicted video ratings on average, individuals differed widely in terms of the extent to which motion energy influenced their ratings of auditory vividness. Using regression analyses, the slope of a function could be quantified for each individual relating the ratings of each video to their motion energy. This individual measure of motion energy sensitivity provides a test of genuineness for vEAR, which is unbiased by semantic associations, and which is underpinned by objective measurement of stimulus characteristics. This measure was distributed smoothly, showing no dichotomous split between individuals who have high versus low motion energy sensitivity (**Figure 2a-b**). ME-sensitivity can therefore occur normally and frequently in a randomly sampled population, supporting our previous estimates of relatively high prevalence of vEAR self-reports (Fassnidge et al., 2019, 2017; Fassnidge & Freeman, 2018), and contrasting with other canonical synaesthesias which are typically more rare (Johnson, Allison, & Baron-Cohen, 2013; Simner et al., 2006). Furthermore, ME-sensitivity reliably predicted answers to our question about previous awareness and also self-ratings of vEAR characteristics, further reinforcing the link between our objective measure of ME-sensitivity and the subjective experience of vEAR.

By linking subjective phenomena with objective measures, our vEAR measure contrasts with other typical tests of genuineness used in synaesthesia research, which rely on objective or subjective measures more exclusively. For example, in the Synaesthetic Stroop test, synaesthetic colour evoked by graphemes can implicitly affect response times to physically coloured letters, however in the absence of a directly related subjective measure, it is debated whether participants who only show objective synaesthesia-like performance really experience synaesthetic phenomena (Bor et al., 2014; Deroy & Spence, 2013). The experience of synaesthesia can be assessed using phenomenological reports or other exclusively subjective measures of genuineness, such as testing consistency of identifying concurrent coloured phosphenes over repeated trials (Bor et al., 2014), however it can be difficult to verify whether such reports reflect genuine perceptual phenomena, strong imagery or even good memory. In contrast, the ME-sensitivity measure correlates subjective ratings of the auditory intensity directly with an objective measure of video motion energy. A high correlation implies that subjective ratings are strongly predicted by the objective stimulus properties; a low correlation implies either that there are no reported sensations, or that they cannot be attributed to objectively measured stimulus characteristics (at least those measure here). ME-sensitivity therefore provides an objective validation and quantification of a subjective phenomenon. Furthermore, it also allows us to begin to investigate the physiological basis for such phenomena, discussed further below.

As we have argued before (Fassnidge et al., 2019, 2017; Fassnidge & Freeman, 2018), the apparent normality and prevalence of vEAR, and also its broad pattern of trait associations, suggests that this form of synaesthesia may depend on systemic variables affecting cortical excitability or disinhibition (Grossenbacher & Lovelace, 2001; Lalwani & Brang, 2019), rather than depending exclusively on rare and specific patterns of anatomical cross-connectivity (Bargary & Mitchell, 2008; Baron-Cohen, 1996; Hubbard & Ramachandran, 2005; Tomson et al., 2011). Here we tested the role of inhibition using a psychophysical measure of surround suppression (Chubb et al., 1989; Xing & Heeger, 2001), finding that participants who made overall higher video ratings tended to show weaker surround suppression. Weaker surround suppression may result from a reduction of inhibitory gain control in early visual cortex (Heeger, 1992). Thus, the present association with vEAR suggests that auditory representations, and/or the connections between visual, auditory and multisensory areas may be disinhibited along with visual representations (Lalwani & Brang, 2019; Neufeld et al., 2012). A previous attempt to link grapheme-colour synaesthesia to reduced surround suppression was inconclusive (Terhune et al., 2014), however that form of synaesthesia might have weaker dependence on early visual representations, relying more on fusiform and parietal areas (Terhune et al., 2014; van Leeuwen, den Ouden, & Hagoort, 2011). The present research is the first, to our knowledge, to demonstrate that visual surround suppression can provide an independent behavioural marker for the reduction of sensory inhibition in at least one form of synaesthesia. It is interesting that surround suppression also tends to be significantly weaker in schizophrenia (Dakin et al., 2005), which may be associated with a deficit in the inhibitory neurotransmitter GABA (Keverne, 1999; Tibber et al., 2013; Yoon et al., 2009). It is tempting to speculate that imbalance in cortical inhibition relative to excitation, of neurochemical origin, may be one common factor underlying the phenomenon of vEAR, and the experience of multisensory deficits and auditory hallucinations which are a diagnostic symptom of schizophrenia (Deng & Huang, 2006; Jardri et al., 2016).

Two aspect of our results may be particularly informative about the possible mechanisms underlying vEAR. Firstly, our regression analyses showed that surround suppression and ME-sensitivity each predict video ratings independently, with no evidence of any interaction. Secondly, video ratings were associated to each factor in distinct ways mathematically: ME-sensitivity is a multiplicative factor, which determines the gradient of the slope relating video ratings to the physical motion energy of the videos; in contrast, SS is a purely additive factor, associated with the overall magnitude of video rating across all videos regardless of their motion energy, and not interacting with the effect of ME-sensitivity. We can attempt to explain these features of the results in the context of a minimalistic conceptual model, where motion energy signals are first transduced in visual cortex with varying gain and thresholds, then relayed to auditory cortex via interconnections of variable weights, before finally triggering a response in auditory cortex, again with varying gain and thresholds.

In this model, ME-sensitivity might relate to factors which could multiplicatively gate the transfer of ME signals between visual and auditory areas by weighting the mutual interconnections; alternatively, ME-sensitivity might modulate the output gain within these areas, thus amplifying or suppressing their response to incoming motion-energy signals. The independent effects of ME-sensitivity relative to SS suggest that ME-sensitivity is not directly related to factors relating to visual inhibition and disinhibition, at least in the early visual system; this result also weighs against the inhibitory role of GABA given its putative role in visual surround suppression (Tibber et al., 2013; Yoon et al., 2009), for otherwise ME-sensitivity and SS effects should be found to interact. An alternative gain-modulating mechanism underlying ME-sensitivity might be an overexpression of the neurotransmitter glutamate, which appears to be elevated in the visual cortex of grapheme-colour synaesthetes and those susceptible to electromagnetically-induced visual phosphenes (Terhune et al., 2015). Independently, reduced SS in vEAR individuals might relate to a reduction of GABA-mediated inhibition that increases input gain, or lowers the threshold in auditory areas for responding to ME signals of visual origin, thus generally increasing the effective intensity of ME signals. Such a shift might then appear to affect video ratings of ME signals of different intensities additively. An alternative possibility is that disinhibition in auditory cortex might increase spontaneous auditory activity, perhaps providing greater raw material for hallucination-like auditory sensations (Kumar et al., 2014; Northoff & Qin, 2011), or allowing neural activity to cross a threshold into awareness via stochastic resonance (Lalwani & Brang, 2019). A similar mechanism might also account for the converse phenomenon of auditory-induced phosphenes, where visual areas respond more sensitively to auditory signals (Bolognini, Senna, Maravita, Pascual-Leone, & Merabet, 2010).

As well as showing independent influences on video ratings, SS and ME-sensitivity each appeared to correlate with different clusters of traits. The use of reverse-coding of survey questions in this study helps to argue against the possibility that such correlations were caused by acquiescence bias, where some participants might have tended to respond generally more positively than others. ME-sensitivity was associated with most of the traits we probed (in decreasing order of the magnitude of the slope relating trait to ME-sensitivity: vEAR self-rating, auditory-evoked phosphenes, earworms, migraine, pattern glare, tinnitus, musicality, and insomnia), with the exception of two (photic sneezing and speech-in-noise comprehension). We can therefore consider the possibility that multiplicative gain-control is a common factor that explains not only ME-sensitivity but this broader set of associated traits, by modulating cortical excitability and sensory sensitivity. This would be consistent with previous research identifying a role for cortical excitability in migraine aura (Palmer et al., 2000; Tibber et al., 2014), pattern glare (Wilkins et al., 1984), insomnia (Van Der Werf et al., 2010), tinnitus (Kaltenbach, 2011), and visual phosphenes (Jacobs et al., 1981; Lessell & Cohen, 1979; Nair & Brang, 2019), as well as EEG evidence that vEAR is associated with stronger early responses to visual stimulation (Rothen et al., 2017). Our questions about musicality and earworms were also selected on the assumption that greater sensitivity to musical patterns, and experiences of involuntary musical imagery might result from greater excitability and spontaneous activity of areas involved in processing the patterns of sound (Griffiths, 2000; Kumar et al., 2014). The above findings are in agreement with other experimental evidence that visual cortical excitability can modulate grapheme-colour synaesthesia (Terhune, Tai, Cowey, Popescu, & Cohen Kadosh, 2011), and such excitability increases following intensive training with grapheme-colour associations (Rothen, Schwartzman, Bor, & Seth, 2018).

In contrast with ME-sensitivity, the traits associated with reduced surround suppression appear much more selective, including only vEAR self-ratings, auditory-evoked phosphenes, and musicality. These traits all seem to involve crossmodal interactions, either from vision to audition (vEAR), and from audition to vision (phosphenes), while musicianship may generally require a high degree of audiovisual integration (Tsay, 2013). It is particularly interesting that in our previous brain-stimulation study (Fassnidge et al., 2019), our sample of highly-trained musicians showed evidence of reduced inhibition (or increased cooperation) between visual and auditory cortices, as well as overall a greater prevalence of vEAR experiences. In sum, this clustering of traits is consistent with our previous proposal that vEAR is characterised by a reduction of mutual inhibition between and within auditory and visual modalities, which may weaken surround suppression, but also reinforces richer crossmodal interactions and the propensity for experiencing synaesthesia-like sensory phenomena.

In conclusion, this study has validated an objective test of vEAR genuineness, which relates the physical characteristics of visual stimuli to subjective reports of auditory sensations, underpinned by a model of motion energy transduction in early visual cortex. Furthermore, this research has contributed to understanding the possible mechanisms underlying this phenomenon as well as other traits and sensory phenomena with which it is associated. In particular it has been proposed that vEAR may be characterised by two independent mechanisms: firstly higher sensory gain, which functions to multiplicatively amplify motion energy signals and/or their transfer across modalities; secondly reduced inhibition between modalities which may function to lower the threshold for experiencing visually-evoked auditory sensations, as well as auditory-evoked phosphenes. Finally, each of these routes to vEAR are associated with different clusters of traits including musicality, tinnitus, pattern glare, and migraine, pointing to a possible common basis for understanding a wide range of different perceptual phenomena and comorbidities. Most intriguingly, the reduction of surround suppression that we observed in vEAR may have parallels with similar reduction in suppression in schizophrenia, pointing to a possible common disinhibitory framework for understanding the neural basis for spontaneous auditory sensations in both healthy and pathological populations.

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Table 1 Alternative wordings of trait questions in vEAR survey

TRAIT	POSITIVE STATEMENT	NEGATIVE STATEMENT
MUSICALITY	*I have a good ear for music*	*I do not have a good ear for music* [1]
TINNITUS	*I suffer from tinnitus*	*I do not suffer from tinnitus* [1]
PHOSPHENES	*I have experienced vivid flashes evoked by sounds*	*I have never experienced flashes evoked by sounds* [1]
EARWORMS	*I very frequently experience earworms*	*I never experience earworms* [1]
VEAR	*I can watch visual movement or flashing without experiencing sounds in my head* [1]	*I cannot watch visual motion or flashing without experiencing vivid sounds in my head*
MIGRAINE	*I get migraines very frequently*	*I never experience migraines*
AURA[2]	*When I get migraines, I usually experience visual disturbances*	*When I get migraines, I never experience visual disturbances*
PATTERN GLARE	*I can look at certain high contrast repetitive patterns without experiencing discomfort or visual distortions* [1]	*I cannot look at certain high contrast repetitive patterns without experiencing discomfort or visual distortions.*
PHOTIC SNEEZING[1]	*I can walk in bright sunshine without experiencing the urge to sneeze* [1]	*I cannot walk in bright sunshine without experiencing the urge to sneeze*
SPEECH IN NOISE	*I am bad at following conversations when there is background noise*	*I am good at following conversations when there is background noise* [1]
INSOMNIA	*I find it hard to sleep at night*	*I find it easy to sleep at night* [1]

[1] *reverse-coded*

[2] *response options included 'not applicable'*

Table 2 Pearson's correlations of video ratings with trait ratings

	Positively-worded	**Negatively-worded**	**Fisher z**[2]
Musicality	r(4566) = 0.201, p<0.001[1]	r(4662) = 0.086, p<0.001	z = 5.643, p<0.001
Tinnitus	r(4656) = 0.144, p<0.001	r(4572) = 0.102, p<0.001	z = 2.054, p=0.362
Phosphenes	r(4597) = 0.288, p<0.001	r(4631) = 0.206, p<0.001	z = 4.193, p<0.001
Earworm	r(4594) = 0.232, p<0.001	r(4634) = 0.043, p=0.037	z = 9.284, p<0.001
vEAR	r(4623) = 0.455, p<0.001	r(4605) = 0.323, p<0.001	z = 7.508, p<0.001
Migraine	r(4632) = 0.130, p<0.001	r(4596) = 0.119, p<0.001	z = 0.522, p=1.000
aura	r(2721) = 0.105, p<0.001	r(2574) = 0.084, p<0.001	z = 0.763, p=0.998
PatternGlare	r(4562) = 0.184, p<0.001	r(4666) = 0.188, p<0.001	z = 0.215, p=1.000
PhoticSneezing	r(4633) = 0.102, p<0.001	r(4595) = 0.105, p<0.001	z = 0.179, p=1.000
Conversations	r(4710) = 0.110, p<0.001	r(4518) = 0.053, p=0.004	z = 2.747, p=0.064

[1] *Bonferonni corrected*
[2] *Comparison of correlation coefficients*

Table 3 Regressions of each trait against Motion Energy sensitivity (ME) and Surround Suppression (SS)

	Regression							Partial correlation			
Trait	**ME slope**[1]	**ME t**	**ME p_{bonf}**[2]	**SS slope**	**SS t**	**SS p_{bonf}**	**Rsq**	**ME r**	**ME p_{bonf}**	**SS r**	**SS p_{bonf}**
Musicality	0.054	4.184	<0.001	-0.008	-3.730	0.002	0.003	0.046	>.001	-0.04	0.001
Tinnitus	0.059	3.823	<0.001	-0.004	-1.526	0.776	0.002	0.043	>.001	-0.011	0.974
Phosphenes	0.082	5.322	<0.001	-0.008	-3.161	0.017	0.004	0.068	>.001	-0.028	0.081
Earworm	0.077	5.674	<0.001	0.001	0.565	1.000	0.004	0.078	>.001	-0.008	0.999
vEAR	0.139	10.177	<0.001	-0.008	-3.625	0.003	0.013	0.134	>.001	-0.03	0.045
Migraine	0.066	4.160	<0.001	0.001	0.226	1.000	0.002	0.043	>.001	0.006	1
aura	0.036	1.661	0.674	0.004	1.258	0.924	0.001	0.03	0.277	0.022	0.704
PatternGlare	0.060	4.117	<0.001	-0.002	-0.947	0.990	0.002	0.052	>.001	-0.002	1
PhoticSneezing	0.040	2.460	0.143	-0.005	-2.065	0.354	0.001	0.024	0.233	-0.011	0.979
Conversations	0.032	2.202	0.266	0.006	2.398	0.167	0.001	0.027	0.091	0.022	0.302
Insomnia	0.051	3.361	0.009	-0.006	-2.433	0.153	0.002	0.039	0.002	-0.025	0.172

[1] *Coefficients from the regression equation:* $Rating_{trait} = ME + SS + \varepsilon$

[2] *All p values are Bonferroni corrected*