FURTHER READING

Alvarez, J.P., Furumizu, C., Efroni, I., Eshed, Y., and Bowman, J.L. (2016). Active suppression of a leaf meristem orchestrates determinate leaf growth. eLife *5*, e15023.
Bharathan, G., Goliber, T.E., Moore, C., Kessler, S., Pham, T., and Sinha, N.R. (2002). Homologies in leaf form inferred from *KNOXI* gene expression during development. Science *296*, 1858–1860.
Bhatia, N., Runions, A., and Tsiantis, M. (2021). Leaf shape diversity: from genetic modules to computational models. Annu. Rev. Plant Biol. *72*, 325–356.
Blein, T., Pulido, A., Vialette-Guiraud, A., Nikovics, K., Morin, H., Hay, A., Johansen, I.E., Tsiantis, M., and Laufs, P. (2008). A conserved molecular framework for compound leaf development. Science *322*, 1835–1839.
Coen, E., Kennaway, R., and Whitewoods, C. (2017). On genes and form. Development *144*, 4203–4213.
Eshed Y., Baum, S.F., Perea, J.V., and Bowman, J.L. (2001). Establishment of polarity in lateral organs of plants. Curr. Biol. *11*, 1251–1260.
Kierzkowski, D., Runions, A., Vuolo, F., Strauss, S., Lymbouridou, R., Routier-Kierzkowska, A.L., Wilson-Sánchez, D., Jenke, H., Galinha, C., Mosca, G., *et al.* (2019). A growth-based framework for leaf shape development and diversity. Cell *177*, 1405–1418.
Kimura, S., Koenig, D., Kang, J., Yoong, F.Y., and Sinha, N. (2008). Natural variation in leaf morphology results from mutation of a novel *KNOX* gene. Curr. Biol. *18*, 672–677.
Maugarny-Calès, A., and Laufs, P. (2018). Getting leaves into shape: a molecular, cellular, environmental and evolutionary view. Development *145*, dev161646.
Ori, N., Cohen, A.R., Etzioni, A., Brand, A., Yanai, O., Shleizer, S., Menda, N., Amsellem, Z., Efroni, I., Pekker, I., *et al.* (2007). Regulation of *LANCEOLATE* by *miR319* is required for compound-leaf development in tomato. Nat. Genet. *39*, 787–791.
Richardson, A.E., Cheng, J., Johnston, R., Kennaway, R., Conlon, B.R., Rebocho, A.B., Kong, H., Scanlon, M.J., Hake, S., and Coen, E. (2021). Evolution of the grass leaf by primordium extension and petiole-lamina remodeling. Science *374*,1377–1381.
Shani, E., Burko, Y., Ben-Yaakov, L., Berger, Y., Amsellem, Z., Goldshmidt, A., Sharon, E., and Ori, N. (2009). Stage-specific regulation of *Solanum lycopersicum* leaf maturation by class 1 KNOTTED1-LIKE HOMEOBOX proteins. Plant Cell *21*, 3078–3092.
Vlad, D., Kierzkowski, D., Rast, M.I., Vuolo, F., Dello Ioio, R., Galinha, C., Gan, X., Hajheidari, M., Hay, A., Smith, R.S., *et al.* (2014). Leaf shape evolution through duplication, regulatory diversification, and loss of a homeobox gene. Science *343*, 780–783.
Waites, R., Selvadurai, H.R.N., Oliver, I.R., and Hudson, A. (1998). The *PHANTASTICA* gene encodes a MYB transcription factor involved in growth and dorsoventrality of lateral organs in *Antirrhinum.* Cell *93*, 779–789.
Whitewoods, C.D., Gonçalves, B., Cheng, J., Cui, M., Kennaway, R., Lee, K., Bushell, C., Yu, M., Piao, C., and Coen, E. (2020). Evolution of carnivorous traps from planar leaves through simple shifts in gene expression. Science *367*, 91–96.

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Undetectable very-low frequency sound increases dancing at a live concert

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Does low frequency sound (bass) make people dance more? Music that makes people want to move tends to have more low frequency sound, and bass instruments typically provide the musical pulse that people dance to[1]. Low pitches confer advantages in perception and movement timing, and elicit stronger neural responses for timing compared to high pitches[2], suggesting superior sensorimotor communication. Low frequency sound is processed via vibrotactile[3] and vestibular[4] (in addition to auditory) pathways, and stimulation of these non-auditory modalities in the context of music can increase ratings of groove (the pleasurable urge to move to music)[3], and modulate musical rhythm perception[4]. Anecdotal accounts describe intense physical and psychological effects of low frequencies, especially in electronic dance music[5], possibly reflecting effects on physiological arousal. We do not, however, know if these associations extend to direct causal effects of low frequencies in complex, real-world, social contexts like dancing at concerts, or if low frequencies that are not consciously detectable can affect behaviour. We tested whether non-auditory low-frequency stimulation would increase audience dancing by turning very-low frequency (VLF) speakers on and off during a live electronic music concert and measuring audience members' movements using motion-capture. Movement increased when VLFs were present, and because the VLFs were below or near auditory thresholds (and a subsequent experiment suggested they were undetectable), we believe this represents an unconscious effect on behaviour, possibly via vestibular and/or tactile processing.

People attending a performance by the electronic music duo Orphx at the LIVELab were recruited for the study. Participants gave informed consent, were fitted with motion-capture marker headbands, and completed pre- and post-concert questionnaires (see Supplemental information). We turned VLF speakers (8–37 Hz) on and off every 2.5 minutes over 55 minutes of the performance (Figure 1D), calculated head movement speed (the three-dimensional path length per sampling unit of time) for each participant in each of the eighteen segments, and compared average normalized movement while VLFs were ON vs. OFF. Our data show that audience participants moved more, on average by 11.8%, while VLFs were ON vs. OFF ($t(42) = 5.32$, $p < 0.0001$; $d = 0.81$; Figure 1E).

Post-concert questionnaire data indicated that participants felt bodily sensations associated with bass frequencies during the concert, and that these were pleasurable and contributed to the urge to move (all $p < 0.001$). However, the bodily sensations were not perceived as stronger than at similar concerts ($p = 0.49$). Together, these results reflect associations between bass, dancing, and pleasure in electronic dance music, consistent with previous reports[5], but also that the bodily sensations apparent to participants were not elicited by the VLFs (most concerts do not use VLF speakers and participants indicated bodily sensations were similar to other concerts).

To confirm that the VLFs were not consciously detectable, 17 new participants (one of whom participated in the concert experiment) completed a two-alternative forced choice task using the same VLF speakers in the LIVELab. On each trial, participants heard two pairs of 3.5 s excerpts from the concert audio and indicated which pair's excerpts were different (all excerpts in the trial were identical except for the presence or absence of VLFs in one excerpt). Participants performed at chance (mean 49.8% correct, SD = 4.56%), and a Bayesian *t* test on participants' rates of correct

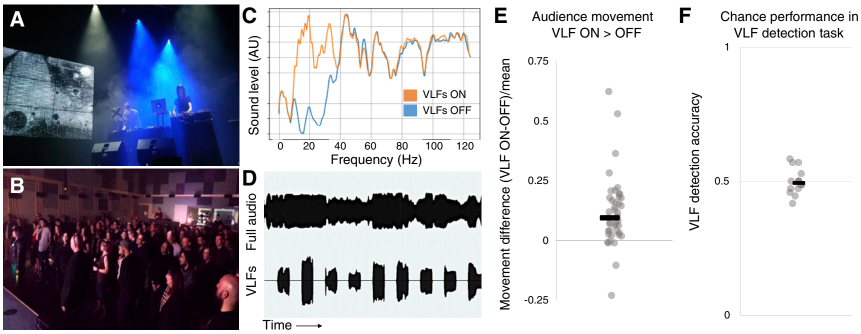

Figure 1. Audience members at an electronic music performance moved more when very-low frequencies were present vs. absent.

(A) Orphx performing at the LIVELab. (B) Audience during the concert. (C) Spectral power in concert audio during VLF ON (orange) and OFF (blue). (D) Waveforms of the concert audio (top) and the VLFs (bottom) from the 55-minute period of data collection. (E) Differences in audience participants' normalized movement (VLF ON – OFF) and group mean (black horizontal bar). (F) Participant performance in the VLF detection experiment.

responses indicated substantial evidence for the null hypothesis — that participants could not detect the presence/absence of VLFs (n = 17; prior = Cauchy distribution centred on 0 with width = 0.707; BF_{0+} = 4.36; Figure 1F). It should be noted that two experimenters familiar with the VLF manipulation and the purpose of this follow-up experiment participated in it and performed at chance (both 50% correct). Omitting their data has a negligible effect, only reducing the Bayes factor slightly (BF_{0+} = 4.12).

These results demonstrate that a complex, social behaviour — dance — can be increased in intensity by VLFs without participants' awareness. This result exceeds the previously known associations between bass and dance, demonstrating a large and highly reliable effect in a context of maximal ecological validity.

Vibrotactile and vestibular systems process low frequency sound, have close links to the motor system, and can affect groove ratings, spontaneous movement, and rhythm perception. Because of these connections, and because VLFs were below or near auditory threshold, these non-auditory sensory pathways were likely involved in the observed effect of VLFs on dancing at a live concert by contributing salient cross-modal cues to the motor system.

One theory suggests the vestibular system in particular has a fundamental role in human perception of low frequencies, musical rhythm, and the urge to move to music, in part due to vestibular-autonomic effects[4]. Our study is consistent with that theory, although it was not a direct test of it.

Some VLFs were above the predicted perceptual thresholds, although consciously undetectable. Because VLFs were relatively near thresholds (that were determined in silence) whereas non-VLFs were far above thresholds (see supplemental material), we believe that auditory masking of the VLFs contributed to their being undetectable.

The undetectable nature of the VLFs shows that the causal relationship between bass and dancing does not reflect an explicit association — that is, it is highly unlikely that audience members identified when VLFs were activated and responded by consciously deciding to dance more (despite having a general association of bass, movement, and pleasure). The implicit nature of the response suggests involvement of subcortical pathways from sound to behaviour, possibly including modulation of the reward system, whose activity is associated with groove[6] and movement vigor[7], and/or timing dynamics in the motor system via basal ganglia[8]. While culture and individual experience may or may not influence the extent to which VLFs influence dancing and movement, their undetectable nature suggests a relatively low-level pathway by which low frequencies influence movement and dancing, in turn suggesting a fundamental aspect of human music cognition and dance behaviour.

SUPPLEMENTAL INFORMATION

Supplemental information includes more detailed description of the VLF manipulation and other methodological details, and results from additional analyses, and links to data, and can be found with this article online at https: //doi.org/10.1016/j.cub.2022.09.035.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Stupacher, J., Hove, M.J., and Janata, P. (2016). Audio features underlying perceived groove and sensorimotor synchronization in music. Music Percept. *33*, 571–589.
2. Lenc, T., Keller, P.E., Varlet, M., and Nozaradan, S. (2018). Neural tracking of the musical beat is enhanced by low-frequency sounds. Proc. Natl. Acad. Sci. USA *115*, 8221–8226.
3. Hove, M.J., Martinez, S.A., and Stupacher, J. (2020). Feel the bass: Music presented to tactile and auditory modalities increases aesthetic appreciation and body movement. J. Exp. Psychol. Gen. *149*, 1137.
4. Todd N.P.M., and Lee, C.S. (2015). The sensory-motor theory of beat induction 20 years on: A new synthesis. Front. Hum. Neurosci. *9*, 444.
5. Jasen, P.C. (2016). Low End Theory: Bass, Bodies and the Materiality of Sonic Experience (New York, NY: Bloomsbury Publishing).
6. Matthews, T.E., Witek, M.A., Lund, T., Vuust, P., and Penhune, V.B. (2020). The sensation of groove engages motor and reward networks. NeuroImage *214*, 116768.
7. Shadmehr, R., and Ahmed, A.A. (2020). Vigor: Neuroeconomics of Movement Control (Cambridge, MA: MIT Press).
8. Cannon, J.J., and Patel, A.D. (2020). How beat perception co-opts motor neurophysiology. Trends Cogn. Sci. *25*, 137–150.

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