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Report

Current Biology

A Neural Basis for Contagious Yawning

Highlights

- Instruction to resist yawning increases the urge to yawn and alters yawn expression
- Instruction to resist yawning does not alter the individual propensity for yawning
- TMS measures of motor excitability and physiological inhibition predict yawning

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In Brief

Contagious yawning (CY) is triggered involuntarily when we observe another person yawn. Brown et al. use TMS to investigate the neural basis for CY. They demonstrate that TMS measures of motor cortical excitability and physiological inhibition are significant predictors of CY and account for approximately 50% of the variability in CY.

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Current Biology
Report

A Neural Basis for Contagious Yawning

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SUMMARY

Contagious yawning, in which yawning is triggered involuntarily when we observe another person yawn, is a common form of echophenomena—the automatic imitation of another's words (echolalia) or actions (echopraxia) [1]. The neural basis for echophenomena is unknown; however, it has been proposed that it is linked to disinhibition of the human mirror-neuron system [1–4] and hyper-excitability of cortical motor areas [1]. We investigated the neural basis for contagious yawning using transcranial magnetic stimulation (TMS). Thirty-six adults viewed video clips that showed another individual yawning and, in separate blocks, were instructed to either resist yawning or allow themselves to yawn. Participants were videoed throughout and their yawns or stifled yawns were counted. We used TMS to quantify motor cortical excitability and physiological inhibition for each participant, and these measures were then used to predict the propensity for contagious yawning across participants. We demonstrate that instructions to resist yawning increase the urge to yawn and alter how yawns are expressed (i.e., full versus stifled yawns) but do not alter the individual propensity for contagious yawning. By contrast, TMS measures of cortical excitability and physiological inhibition were significant predictors of contagious yawning and accounted for approximately 50% of the variability in contagious yawning. These data demonstrate that individual variability in the propensity for contagious yawning is determined by cortical excitability and physiological inhibition in the primary motor cortex.

RESULTS

Contagious yawning has been demonstrated previously in humans, chimpanzees, Old World monkeys, and dogs, and can be triggered by hearing or seeing another individual yawning [5]. Furthermore, watching or hearing another individual yawn activates a network of brain regions that are associated with motor imitation and empathy [3, 6]. For this reason, contagious yawning has frequently been linked to the operation of the human mirror-neuron system (MNS) [3, 6], which is thought to play a key role in action understanding, empathy, and the synchronization of group social behavior [7]. However, functional brain imaging studies have provided mixed evidence in support of this proposal, and have reported that core regions of the human MNS are not in fact activated during contagious yawning [3, 6]. Furthermore, although the propensity for contagious yawning varies across individuals, a recent study has shown it to be stable across time (i.e., measurement sessions) and also uncorrelated with empathy scores [8].

Alternatively, it has been proposed that echophenomena, including contagious yawning, may be generated automatically by ethological releasing mechanisms responsible for triggering stereotyped motor acts [9], and that the propensity for echophenomena may be linked to individual differences in cortical motor excitability [1]. This proposal is consistent with the observation that echophenomena are observed within a few weeks of birth but decrease after around 3 years of age, consistent with the development of self-regulatory mechanisms and reduced automatic imitation of observed actions. It is also consistent with the demonstration that echophenomena are observed in a wide range of clinical conditions linked to increased cortical excitability and/or decreased physiological inhibition (e.g., epilepsy, dementia, autism, Tourette syndrome) [1].

In the current study, we tested the hypothesis that the propensity for contagious yawning was positively associated with motor excitability. Specifically, we investigated whether individual differences in baseline measurements of motor cortical excitability and physiological inhibition were associated with the propensity for contagious yawning. Prior to commencing the contagious yawning experiment, transcranial magnetic stimulation (TMS) measures of cortical excitability and physiological inhibition were recorded from the left primary motor cortex (M1) for each participant and subsequently used to predict propensity for contagious yawning.

The design of the experimental task is illustrated in Figure 1A. Participants viewed video clips that showed another individual yawning and, in separate blocks, were instructed to either resist yawning or allow themselves to yawn. Blocks 1 and 2 were completed without non-invasive electrical brain stimulation, but during blocks 3 and 4 transcranial electrical stimulation (tES) was delivered continuously to the supplementary motor area (SMA) region of the scalp. It should be noted, however, that for

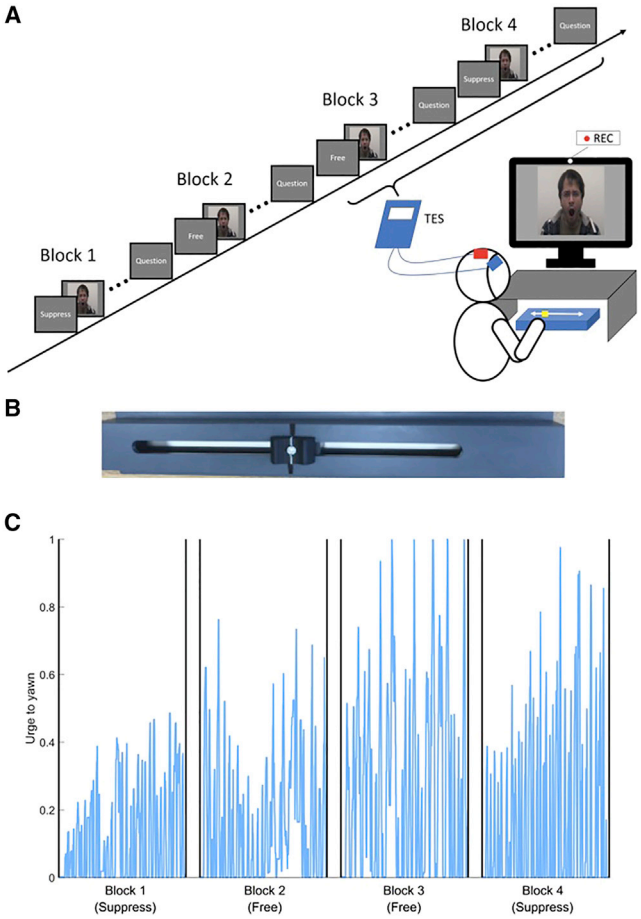

Figure 1. Design of the Behavioral Task

(A) Participants viewed video clips that showed another individual yawning and, in four separate blocks, were instructed to either resist or permit themselves to yawn. Participants were videoed throughout and their yawns or stifled yawns were counted. During the latter two blocks (3 and 4), excitatory non-invasive electrical brain stimulation (anodal transcranial direct current stimulation [tDCS] or transcranial random noise stimulation [tRNS]) was delivered continuously to the cortical SMA region (contrasted with sham stimulation). To ensure that participants paid attention to the videos, they were required to answer a question (e.g., How many people in the videos were wearing glasses?) after each block.

(B) Illustration of the slider device used to continuously record each participant's self-estimate of their current urge to yawn (see text for details).

(C) A representative example of one individual's self-estimated urge to yawn across the four separate blocks of the behavioral task.

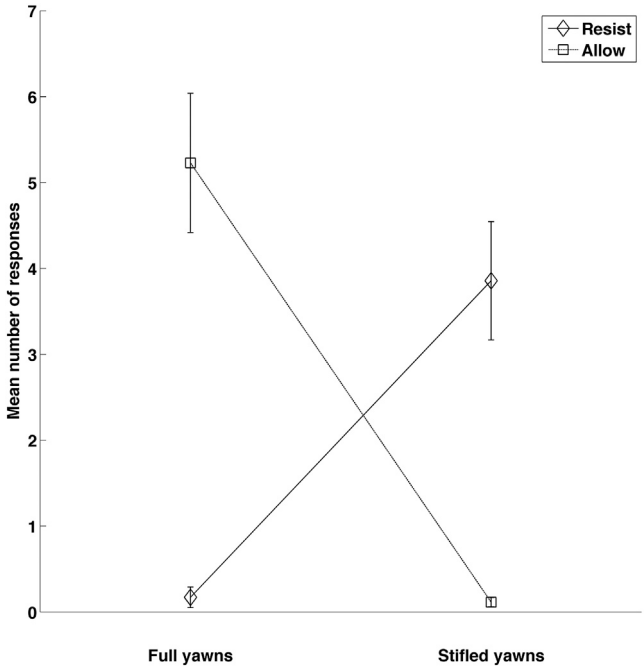

Figure 2. Effect of Instruction

Illustration of the effect of instructing participants to either allow themselves to yawn or resist yawning on the mean number of full and stifled yawns observed. Error bars represent the SEM.

brevity, only data recorded from blocks 1 and 2 will be reported in this paper, and that the effects of tES on the propensity for contagious yawning will be reported elsewhere.

Participants were videoed throughout, and their yawns and stifled yawns were counted. In addition, throughout the experiment the intensity of each participant's perceived urge to yawn was continuously recorded using a slider device that the participant operated using his or her right index finger (Figure 1B). This device delivered a continuous voltage signal that indexed change over time in self-estimated intensity in the perceived urge to yawn. Representative data from one individual are presented in Figure 1C.

Effects of Instruction on Yawning Behavior

To determine whether the instruction to resist yawning had an effect on yawning behavior, we examined the number of full and stifled yawns observed during the first two blocks of trials. Data were analyzed using a two-way repeated-measures ANOVA with the factors Instruction condition (allow versus resist yawning) and Yawn response (full versus stifled yawns). The ANOVA revealed no significant main effects (maximum $F(1,34) = 2.22$, $p > 0.14$) but a significant Instruction x Response interaction ($F(1,34) = 54.29$, $p < 0.0001$). Relevant means are presented in Figure 2. The simple effects of this interaction demonstrated that whereas full yawns were substantially reduced following the instruction to resist yawning (means: allow condition, 5.23; resist condition, 0.17; $t(34) = 6.31$, $p < 0.0001$; effect size [Hedges' G] = 1.46), stifled yawns were significantly increased by the instruction to resist yawning (means: allow condition, 0.11; resist condition, 3.86; $t(34) = 5.51$, $p < 0.0001$; effect size [Hedges' G] = 1.28). These data confirm that the instruction to suppress contagious yawning was only partially successful, and led to a significant decrease in full yawns but an increase in the number of stifled yawns observed (means: full yawns, 0.17; stifled yawns, 3.86; $t(34) = -5.13$, $p < 0.0001$; effect size [Hedges' G] = −1.25).

To further determine whether the instruction to resist yawning had an effect on yawning behavior, we examined the sum total of full and stifled yawns observed during the first two blocks of trials. This analysis revealed that the means were not significantly different from one another (resist, 4.03; allow, 5.34; $t(34) = -1.489$ $p > 0.05$). This finding indicates that the instruction to resist yawning significantly increases the urge to yawn

(reported below) and alters how the yawn may be expressed (i.e., stifled yawns rather than full yawns), but it does *not* alter the individual's propensity for yawning. This is consistent with previous reports that although contagious yawning is variable across individuals, an individual's propensity for contagious yawning is nevertheless highly consistent over time. It is also consistent with our finding that the excitability of each individual's motor cortex (described below) is a significant predictor of the propensity for contagious yawning.

Effects of Instruction on Self-Estimates of the Urge to Yawn

We have argued elsewhere that whereas sensory signals may trigger actions outside of awareness, a distinguishing feature of urges for action is that they are chiefly associated with actions that cannot be realized immediately and must be held in check until an appropriate time, when they can be released [10]. To determine whether the instruction to resist yawning led to an increase in perceived urge-to-yawn values in the current study, we compared mean self-reported urge-to-yawn values in the ''allow'' versus ''resist'' blocks of the pre-stimulation period (i.e., blocks 1 and 2). A within-subject t test revealed that urge-to-yawn estimates increased significantly when participants were instructed to resist yawning compared to when they allowed themselves to yawn (pre-stimulation block means: allow, 0.15 units (0–1); resist , 0.18 units (0–1); $t(35) = -1.85$, $p < 0.04$). These data are consistent with the proposal that awareness of urges for action increases in circumstances where actions are suppressed or their execution is delayed [10].

Effects of Motor Excitability and Physiological Inhibition on Propensity for Contagious Yawning

It has been proposed that the propensity for echophenomena such as contagious yawning may be linked to individual variability in cortical motor excitability [1]. To investigate this proposal directly, we used a number of single- and paired-pulse TMS protocols to measure cortical excitability and physiological inhibition within the primary motor cortex of the left hemisphere (contralateral to the dominant right hand). The measurements obtained from each participant consisted of the following: resting motor threshold (RMT); TMS recruitment curve (sometimes referred to as the input-output or IO curve); intracortical facilitation (ICF); short-interval intracortical inhibition (SICI); and long-interval intracortical inhibition (LICI). These measures have been used repeatedly to characterize motor excitability and physiological inhibition [11]. The reader is referred to STAR Methods for methodological details.

To investigate directly whether individual differences in measures of cortical motor excitability and/or physiological inhibition predicted individual variability in the propensity for contagious yawning, we conducted separate stepwise regression analyses of the total number of yawns (i.e., full + stifled) observed from each participant in the allow and resist conditions. The analysis confirmed that TMS measures were not a significant predictor of the total number of yawns recorded in the resist condition (all $p < 0.1$). By contrast, the stepwise regression analysis demonstrated that a model based upon three factors, LICI, RMT, and SICI, could significantly predict and account for close to 50% of the individual variability in the number of full yawns recorded in the allow condition ($F = 10.71$, $p < 0.001$). The order of entry into the model for these factors was as follows: LICI (coefficient = 4.15; t statistic = 3.89; $p = 0.0005$), $F = 6.81$, $p = 0.014$, R-squared value (Rsq) = 0.18, adjusted R-squared value (Adj-Rsq) = 0.15; RMT (coefficient = −0.38; t statistic = −4.33; $p = 0.0002$), $F = 8.65$, $p = 0.001$, Rsq = 0.36, Adj-Rsq = 0.32; and SICI (coefficient = −6.78; t statistic = −3.14; $p = 0.004$), $F = 10.71$, $p < 0.001$, Rsq = 0.52, Adj-Rsq = 0.47. It should be noted that in this stepwise regression, the R-squared values for RMT and SICI are calculated on the residual variance remaining after the LICI and LICI + RMT fits, respectively, have been accounted for.

LICI is a paired-pulse TMS protocol in which two supra-threshold TMS pulses are delivered through a single coil with an inter-stimulus interval (ISI) of 50–200 ms (see STAR Methods). LICI typically leads to a reduction in the size of motor-evoked potentials evoked from a standard TMS pulse, and is typically reported as the ratio of the conditioned over an unconditioned test motor-evoked potential amplitude. LICI is taken to reflect physiological inhibition and is thought to be mediated by GABA-B receptors [12]. The relationship in the current study between LICI and yawning is illustrated Figure 3A. Inspection of this figure clearly illustrates that increased physiological inhibition (i.e., conditioned/unconditioned motor-evoked potential ratio trial values less than 1) is associated with a reduction in the number of yawns observed.

RMT is the amount of stimulation required (expressed as a percentage of maximum stimulator output) to reliably generate a motor-evoked potential motor-evoked potential of a predefined magnitude (typically 50–100 μV) from a target muscle at rest. RMT is thought to reflect the excitability of those corticospinal neurons with the lowest excitation threshold that project to the target muscle [13] and the TMS-induced excitability of cortical-cortical fiber axons [12]; RMT is known to be highly variable between, but not within, individuals [14]. The relationship in the current study between RMT and the residual variance in yawning (i.e., after variance due to 100-ms LICI is accounted for) is illustrated in Figure 3B. Inspection of this figure clearly illustrates that lower motor thresholds are associated with an increased number of yawns.

SICI is a paired-pulse TMS protocol in which two TMS pulses are delivered in rapid succession (1–5 ms ISI) through a single coil. However, in SICI protocols, a standard supra-threshold TMS pulse is preceded by the delivery of a sub-threshold conditioning pulse. SICI typically leads to a reduction in motor-evoked potential amplitudes, and is thought to reflect the operation of GABA-A-mediated inhibitory interneurons acting upon corticospinal neurons [12]. Thus, LICI and SICI are thought to reflect quite different mechanisms of physiological inhibition. In the current study, and in contrast to the findings for LICI, we observed that increased SICI was associated with an increase in the number of yawns observed (Figure 3C). This finding is consistent with the key role that GABA-A-mediated inhibition is thought to play in the control of movement-related brain oscillations. Specifically, movement-related beta oscillation de-synchronization, which is linked to the initiation of movements, has been shown previously to be facilitated by increased GABA-A-mediated inhibition [15].

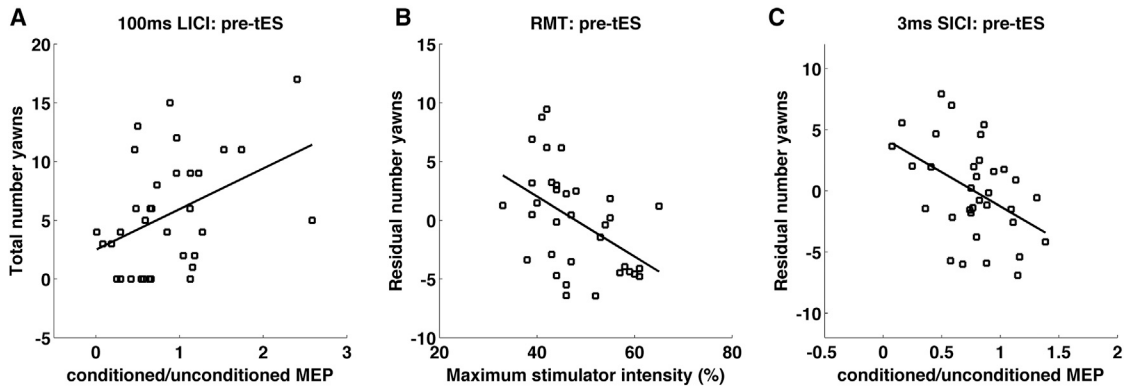

Figure 3. Results of Stepwise Regression Analysis

(A) Scatterplot showing the association between 100-ms LICI values (x axis) and the total number of yawns (stifled + full) recorded in the allow condition (y axis). Note that a ratio value of <1 represents an inhibitory effect of the conditioning pulse (see text for details).

(B) Scatterplot showing the association between the resting motor threshold (RMT) (x axis) and the residual (i.e., unexplained by 100-ms LICI) variance in the total number of yawns recorded in the allow condition (y axis). Note that increased excitability is indexed by a lower RMT value.

(C) Scatterplot showing the association between 3-ms SICI values (x axis) and the residual (i.e., unexplained by 100-ms LICI + RMT) variance in the total number of yawns recorded in the allow condition (y axis). Note that a ratio value of <1 represents an inhibitory effect of the conditioning pulse (see text for details).

Effects of Motor Excitability and Physiological Inhibition: Predicting the Effects of Instruction

The stepwise regression analyses revealed that none of the TMS measures were statistically significant predictors of the number of stifled yawns observed in the resist block (all $p > 0.1$). To investigate this issue further, we ran a further stepwise regression in which we estimated whether the pre-stimulation TMS measures (above) predicted the *difference* in the total number of yawns (i.e., full + stifled yawns) exhibited in the resist versus allow conditions. The analysis revealed a marginally significant effect for RMT ($F = 3.97$, $p < 0.055$, Adj-$R^2 = 0.08$). This indicates that those individuals with a more excitable motor cortex (i.e., lower RMT values) tended to exhibit larger negative differences in the number of yawns observed in the resist − allow subtraction.

Effects of Motor Excitability and Physiological Inhibition on the Urge to Yawn

We conducted a stepwise regression to determine whether any single pre-stimulation TMS measure (i.e., SICI, ICF, LICI, IO slope, or RMT), or combination of TMS measurements, was a significant predictor of the urge to yawn. The answer to this was that they were not (all $p > 0.05$). This suggests that although motor cortical excitability is a significant predictor of the propensity for contagious yawning, it is not a significant driver of, or associated with, the urge to yawn. This finding is in fact consistent with previous accounts that have proposed that the urge for action may be associated primarily with upstream brain areas such as the anterior insular cortex and cingulate motor area (e.g., [10]).

DISCUSSION

We investigated the neural basis for contagious yawning—an example of echophenomena—using non-invasive brain stimulation (TMS) techniques. Contagious yawning can be triggered by seeing another individual yawn [5], but the propensity for contagious yawning, although stable over time, is known to vary across individuals [8]. Here we provide evidence that the propensity for contagious yawning may be triggered automatically and is strongly linked to the cortical excitability of the primary motor cortex. Specifically, TMS was used to quantify baseline cortical excitability and physiological inhibition within the primary motor cortex and to predict behavioral measures of contagious yawning, and we tested the hypothesis that the propensity for contagious yawning was linked to the balance of cortical excitability and physiological inhibition within the primary motor cortex [1].

The key findings from the study can be summarized as follows. First, the instruction to resist yawning proved to be only partially successful. Although it led to a significant decrease in the number of full yawns observed, there was a significant increase in the number of stifled yawns recorded. Furthermore, when the numbers of full and stifled yawns were combined into a single measure, the difference between the resist and allow conditions was not statistically significant. Nonetheless, urge-to-yawn estimates increased significantly when participants were instructed to resist yawning. This is consistent with the proposal that urges for action are chiefly associated with actions that cannot be realized immediately and must be held in check. Together, these findings demonstrate that the instruction to resist yawning significantly increases the urge to yawn and alters how the yawn may be expressed (i.e., stifled yawns rather than full yawns), but it does *not* alter the individual's propensity for yawning.

Second, the propensity for contagious yawning was shown to be strongly predicted by individual variability in TMS measures of cortical motor excitability and physiological inhibition recorded from the hand area of the primary motor cortex.

We suggest that these findings may be particularly important in understanding further the association between motor excitability and the occurrence of echophenomena—observed in a wide range of clinical conditions, e.g., epilepsy, dementia, autism, and Tourette syndrome, that have been linked to increased cortical excitability and/or decreased physiological inhibition [1].

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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AUTHOR CONTRIBUTIONS

G.M.J., S.R.J., B.J.B., D.R., and S.K. conceived and designed the study. B.J.B., H.S., C.B., J.T., and S.K. conducted the study and collected the data. B.J.B., S.K., and S.R.J. conducted the data analyses. B.J.B., S.K., G.M.J., and S.R.J. wrote the paper.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
MATLAB	Mathworks	http://www.mathworks.com
Excel	Microsoft Office	http://www.microsoft.com/UK/Office
VLC media player	Videolan	http://www.videolan,org/vlc
BrainVision software	Brain Vision	http://www.brainvision.com
OBS Studio	Open Broadcaster Software	http://www.obsproject.com
Other		
Magstim Bistim 2 stimulator and 70mm figure-of-eight coil.	N/A	http://www.magstim.com
BrainSight (Rogue Research) neuronavigation system	Brainsight	http://www.rogue-research.com
Custom made Slider Mechanism	Andrew Smith	andrew.smith@nottingham.ac.uk
Ag-AgCl electrodes - H124SG Foam Hydrogel	N/A	N/A

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources may be directed to and will be fulfilled by the Lead Contact, Professor Stephen Jackson (stephen.jackson@nottingham.ac.uk).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Participants

Thirty-six neurologically healthy young adults aged 18-26 years (mean: 20 ± 1.56 years) participated in this study. Prior to the study all participants were screened for transcranial magnetic stimulation (TMS) and transcranial electrical stimulation (tES) safety and informed consent was obtained. Ethical approval was obtained from the University of Nottingham school of psychology research ethics committee. Two subjects were subsequently excluded from TMS data analysis: one due to their not tolerating the TMS procedure for long enough to collect a full data series; and the other due to their SICI response being more than 3 SD from the group mean.

METHOD DETAILS

Study design

The aim of this study was to examine whether propensity for contagious yawning could be predicted by neurophysiological measures obtained from M1 using TMS. TMS measures including RMT, IO curve, SICI, ICF, LICI were obtained. This was then followed by a contagious yawning behavioral paradigm. Participants watched two blocks of video recordings featuring individuals yawning. In each block, participants were asked to either freely yawn or resist yawning. The order of instructions was counterbalanced across participants. In each block two different yawning responses (full yawn and stifle yawns) and urge to yawn were measured. Please note that this study was conducted as part of a larger study. This larger study included four blocks of yawning video viewing and tES was applied continuously during blocks 3 and 4. However, the analysis of contagious yawning in blocks 3 and 4, or the effects of tES, are not included in the current paper and will be reported elsewhere.

TMS

A Magstim Bistim^2, with a 70mm figure of eight branding iron coil, was used to administer TMS to the left M1 in an area corresponding to the first dorsal interosseous (FDI) muscle of the right hand. The motor hotspot was defined as the coil location that elicited maximal motor-evoked potential responses in FDI by positioning the TMS coil over each subjects left motor cortex (M1) at approximately 45°. The coil location was continuously tracked throughout the study, via BrainSight version 2.0 (Rogue Research © 2016) with a template brain scan. EMG responses were recorded using BrainVision system (BrainProducts GmbH, Germany) at a sampling rate of 5000 Hz and band pass filtered (10-2000 Hz). Disposable Ag-AgCl surface electrodes (diameter 24mm) were placed onto the FDI muscle in a standard 'belly-tendon' configuration.

RMT and IO curves

Following localization of the motor hotspot, resting motor threshold (RMT) was obtained. Each subjects RMT was determined as the minimum TMS intensity needed to elicit a FDI generated motor-evoked potential of at least 150–200 μV in a minimum of 5 out of 10 trials. TMS intensities administered ranged from 100% - 150% of RMT and delivered in 10% increments resulting in 6 TMS intensities with an inter-trial interval (ITI) of 5 s. There were a total of 90 trials, which were split into 15 trials per TMS intensity. Trials were administered in a randomized order across the total number of trials. The IO curve measurements were estimated for each individual by calculating the median motor-evoked potential amplitudes for each of the TMS intensities (i.e., 100%–150% of RMT). A linear fit was then applied to the resulting values. Median values were calculated as opposed to the mean in order to limit the effect of non-standard distribution of individual data.

Paired pulse TMS (SICI, LICI, & ICF)

Paired pulse TMS (ppTMS) was performed at four inter-stimulus intervals (ISIs); 1 ms, 3 ms (SICI), 12 ms (ICF) and 100 ms (LICI). For 1 and 3 ms SICI the conditioning stimulus (CS) was set as 55% of RMT, ICF at 75%, and LICI at 100% of RMT. The CS was followed by TS at the intensity yielding 1 mV (SI 1mV) (20 trials per stimulus condition). There were also 60 unconditioned stimuli (total 140 trials). All conditions were delivered in a pseudo-randomized order with an ITI of 6 s. Paired pulse TMS measures were reported at a ratio to unconditioned responses (i.e., conditioned motor-evoked potential/unconditioned motor-evoked potential).

Behavioral task procedure

Directly following TMS procedures the participants completed the contagious yawning behavioral task. Participants were instructed to watch a 20 min (2 blocks) video of actors yawning. In each block, participants were asked to either 'freely yawn' or 'resist yawning'. The order of instruction was counterbalanced across individuals. In both blocks participants were asked to pay close attention to the screen and answer fours questions relating to the actors they would see such as, 'how many actors were wearing glasses'. Answers provided were later used to confirm that they were paying attention to the video clips appropriately. Each question was asked after each block and prior to the next block.

The yawning stimuli video was produced in-house and comprised four 9 min blocks of video clips (total 52 clips) with each clip ranging from 11-20 s in length. Each video clip featured either a female or male actor (aged 20-28 years) spontaneously yawning. Each block of videos was also collated into 12 randomized video sets, which were then counterbalanced across all participants. All videos were shown on an Apple Macintosh desktop (screen size 22 inch) via VLC media player software. Prior to the start of each of the video blocks subjects were instructed to either *'resist the urge to yawn'* or to *'yawn freely'*. In each block both stifle and full yawns were measured.

Video clips were played continuously throughout the 9 min duration with no interval between each clip. However, each block was separated by a 45 s interval. At the end of each block, participants had this 45 s interval to answer the question corresponding to that particular block. For the duration that the video' recording was playing each subjects face was recorded using Open Broadcaster Software.

Each participant's face was video-recorded using the computer's built-in camera and OBS studio. They were also instructed to record their subjective urge to yawn by continuously adjusting a custom-made slider throughout the duration of each block. The length of the slider mechanism was 195mm, which was scaled to give urge readings between 0 (left end-no urge) and 1 (right end-maximum urge). The slider reading was sampled at 32Hz using MATLAB 2010b (Mathworks, USA).

Yawn count procedure

Two naive raters were chosen to watch the covert video recordings and count the number of full yawns (FY) and stifled yawns (SY) displayed by the subjects during each video block. The recordings were blinded in order to prevent the display of the block condition to the raters. The two raters were also required to follow a strict yawn count protocol in order to ensure consistency and reliability.

QUANTIFICATION AND STATISTICAL ANALYSIS

The number of full yawns (FY) and stifled yawns (SY) displayed by the participants during each video block were counted using an agreed yawn count protocol. Yawn counts were collated for each instruction (allow-yawning & resist-yawning) and condition (full & stifled yawns) to allow us to examine the relationship between the TMS physiological parameters and the participants' propensity for contagious yawning. In addition, the participants' subjective urge to yawn ratings for blocks 1 and 2 were also analyzed. Statistical analyses included the following; two-way repeated-measures ANOVA of behavioral data with the factors Instruction condition (allow versus resist yawning) and Yawn response (full versus stifled yawns); within-subject t tests; stepwise regression analysis; and a priori planned independent-group t tests.

DATA AND SOFTWARE AVAILABILITY

Data and software can be obtained from the Lead Contact on request.