



Research Report

Inhibition of the supplementary motor area affects distribution of effort over time



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ABSTRACT

In tasks that extend over time, people tend to exert much effort at the beginning and the end, but not in the middle, exhibiting the stuck-in-the-middle pattern (STIM). To date, little is known about the neural mechanisms underlying this effect. As the supplementary motor area (SMA) was previously implicated in coding prospective task-demands, we tested its role in producing the STIM pattern. Participants first underwent an SMA-localization session in which they tapped their fingers repeatedly while fMRI-scanned. In the next two sessions, before playing a 10-min computer game that measured effort-engagement, participants underwent inhibitory 1-Hz repetitive transcranial magnetic stimulation over the SMA, or over a control precuneus location. Three control experiments and a pretest confirmed that this task yields a STIM, which can be eliminated when the task lacks a salient end-point, or is too short. The results of the main experiment showed a more pronounced STIM following inhibitory SMA stimulation compared to control. A control analysis showed that overall level of effort was similar in both conditions, rendering alternative accounts in terms of motor inhibition unlikely. These findings are consistent with the possibility that the SMA may play a role in moment-to-moment coding of effort value, or in related sub-processes, which can cause effort to be distributed more equally over the course of a task.

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1. Introduction

People often face a need to exert effort through an extended period of time, until they achieve a goal or reach a deadline. For example, employees work until the end of their shift, and video-game players exert effort until they complete a quest. In many such situations, people tend to invest high levels of effort in the beginning and towards the end of the task, and lower levels of effort in its middle. This U-shape pattern of effort allocation has been termed “the stuck-in-the-middle effect” (STIM) and was demonstrated in both laboratory and field behavioral studies (e.g., Bonezzi et al., 2011; Touré-Tillery & Fishbach, 2012, 2015). For example, Bonezzi et al. (2011) had participants correct typos in a series of nine essays. They found that participants corrected typos faster in the 2nd and 8th essays compared to the 5th. As another example, athletes in track-races, swimming, rowing and cycling were found to demonstrate a STIM pattern through their bouts, performing the first and last intervals faster than the middle ones (Foster et al., 2004; McGibbon et al., 2018; Muehlbauer et al., 2010; Tucker et al., 2006).

In general, level of effort is believed to reflect a balance between effort cost and its reward (e.g., Kool & Botvinick, 2014; Morel et al., 2017; Shenhav et al., 2017; Westbrook & Braver, 2015), and by that account, the STIM pattern would reflect higher reward and/or lower cost for effort in the beginning and the end of a task. Consistent with this view, it has been suggested that effort cost increases over time (and correspondingly effort decreases in the course of a task; Kurzban et al., 2013), and that actions are experienced as more rewarding in the beginning and the end of a task, giving rise to the STIM pattern (Bonezzi et al., 2011; Heath et al., 1999; Katzir et al., 2020). Although much is known about the psychological causes of the STIM effect, its neuronal underpinnings remain unknown. The present study aimed to close this knowledge gap, and thereby enrich our understanding of effort allocation processes in general and the STIM pattern in particular.

Recently, non-invasive supplementary motor area (SMA) inhibition has been implicated in perceiving effort as lower. Specifically, Zénon et al. (2015) found that participants reported lower effort and showed less pupil-dilation (a physiological index of effort) while squeezing a handgrip, following inhibitory continuous theta burst stimulation (cTBS) over the SMA compared to a control precuneus stimulation. In addition, participants accepted offers to reproduce an effortful squeeze in return for a given payment more after cTBS to the SMA than to a control location. This latter finding is also consistent with the possibility that inhibition of the SMA caused participants to perceive the level of effort that they exerted as lower. Importantly, the SMA was not implicated in reward-processing per se, which has been found to be associated with activity in other regions such as the orbitofrontal cortex (OFC), dorsolateral prefrontal cortex (dlPFC), ventromedial prefrontal cortex (vmPFC), dorsal anterior cingulate cortex (dACC), and the striatum (e.g., Bonnelle et al., 2015; Burke et al., 2013; Croxson et al., 2009; Lee et al., 2007).

In light of these findings, we hypothesized that inhibiting SMA activity would modulate the STIM pattern of effort allocation. Specifically, in light of the results of (Zénon et al., 2015),

we hypothesized that stimulation to the SMA would make participants perceive effort as less costly. We thought that this would make levels of effort less evenly distributed in the course of the task, and more responsive to proximity to the beginning and the end of the task, and thus predicted a steeper, more pronounced STIM pattern of effort allocation after stimulation to the SMA compared to a control location.

We employed a simple computer game, which we validated in three control experiments and a pretest as a procedure that enables measurement of effort and gives rise to the STIM pattern of effort allocation. In this game, participants control a spaceship and shoot asteroids using the spacebar, with the number of spacebar presses serving as the measure of effort (see Ames & Fiske, 2015 and Control Experiment 1 for a validation of this measure). Participants completed the game after undergoing inhibitory 1 Hz repetitive transcranial magnetic stimulation (rTMS) over the SMA or a control precuneus location (see Materials and Methods).

2. Materials and Methods

2.1. Participants

Twenty-one healthy, right-handed volunteers with no neurological or psychiatric history participated in the study (10 female; $M_{age} = 25$, $SD_{age} = 3.2$). Sample size was determined based on Zénon et al.'s (2015) findings, which indicated over 80% statistical power for the main effect of TMS stimulation site on effort-perception, both in self-report ratings and pupil dilation in a 3 (stimulation condition: M1/SMA/precuneus) X 4 (effort intensity: 10/23/37/50% of maximal voluntary contraction) repeated-measures analysis of variance with 12 participants. In addition, we tested a power curve analysis based on a pilot study of 98 participants who conducted a 15-min block of the spaceship task testing for the minimum sample size needed to obtain a baseline STIM. The analyses revealed that over 95% power can be achieved using a sample of 20 participants.

Three participants were excluded from the study due to artifacts in the MRI scan, TMS discomfort, and meeting the exclusion criterion achieving a score of 3.5 SDs below the group mean in one of the experimental conditions. The final sample thus consisted of 18 participants who completed the three experimental sessions. All participants provided written informed consent and all procedures were approved by the Tel Aviv Sourasky Medical Center and Tel Aviv University's Ethics committees. All procedures were in accordance with approved guidelines of the Helsinki Declaration. Subjects were required to sleep at least 6 h and to avoid alcohol consumption at least 24 h before each of the experimental sessions. Participants' inclusion criteria followed the guidelines of (Rossi et al., 2009). We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.2. Experimental design

Participants were invited to three sessions. In the first session we acquired anatomical MRI scans, as well as a functional MRI

scan to enable future localization for TMS stimulation (see below). During the localizer functional scan, we asked participants to repeatedly perform a sequence of key-presses with the fingers of their left, non-dominant hand as quickly and accurately as possible (Censor et al., 2010; Kami et al., 1995; Karni et al., 1998). Outside of the scanner in the same session, participants were familiarized with playing the spaceship game (15 mins overall). In the second session, between one to seven days after familiarization, half of the participants played the spaceship game right after receiving rTMS to the SMA-proper ('SMA session') and then returned a minimum of 7 days later for the third session, to play the same game right after receiving rTMS to the precuneus, which served as a control site ('control session'). We chose the precuneus as a control site because it is anatomically distinct from the target-SMA stimulation site [as opposed to a vertex control location] and thus has been used as a control stimulation site in studies that applied TMS to either the SMA or the pre-SMA (Duque et al., 2013; Koch et al., 2005; Kwan et al., 2007; Soutschek et al., 2013; Zènon et al., 2015). The other half of participants conducted the SMA and the control sessions in a reverse order (Fig. 1A). In all sessions, participants completed a subjective performance questionnaire, and two measurements of affect. Namely, they filled two positive and negative affect schedules (PANAS) questionnaires after completing the spaceship task: one referring to their affective state at the moment, and one referring to their affective state while playing the spaceship game.

2.3. Task

Prior to each session, we presented participants with the following instructions:

"In the middle of the screen there is a spaceship that you will have to control. This spaceship is rotated using the left and right arrow keys. You can also make it accelerate using the up key, but notice that the more you accelerate the harder it is to stop the spaceship, as there are no brakes or reverse keys. If you do not press any key, a moving spaceship would drag into a halt. If the spaceship moves out of the screen, it will reappear on the opposite side. The spaceship fires projectiles when you press the spacebar. There is no limitation on the number of projectiles available, but their range is highly limited. These projectiles reappear in the opposite side of the screen if they are shot beyond its borders. Once the experiment begins, asteroids appear randomly on the screen. If you hit an asteroid using the spaceship's projectiles, you will gain ten points, which will be added to your score (the total score will be visible on the top-right corner of the screen), but if you collide with an asteroid, you will lose five points. Your task is to gain as many points as you can. The session will end when the countdown timer at the top of the screen reaches zero and you will be stopped."

There was a maximum of 13 asteroids on the screen. After an accurate shot, the asteroid disappeared, and another one appeared in a random place on the screen after 500 msec. Fig. 1B presents a sample screen from the task. The exact time of each spacebar press was recorded, and the number of spacebar presses served as the dependent variable. Overall scores for each condition were also recorded. We presented participants with a bar that indicated the time left for the block. Each block lasted 10 mins.

We told participants that for each session, the top-performers (participants who pass a predetermined score criterion) would get a bonus of 20 New-Israeli-Shekels (~6 USD). The bonus payment was delivered to participants after

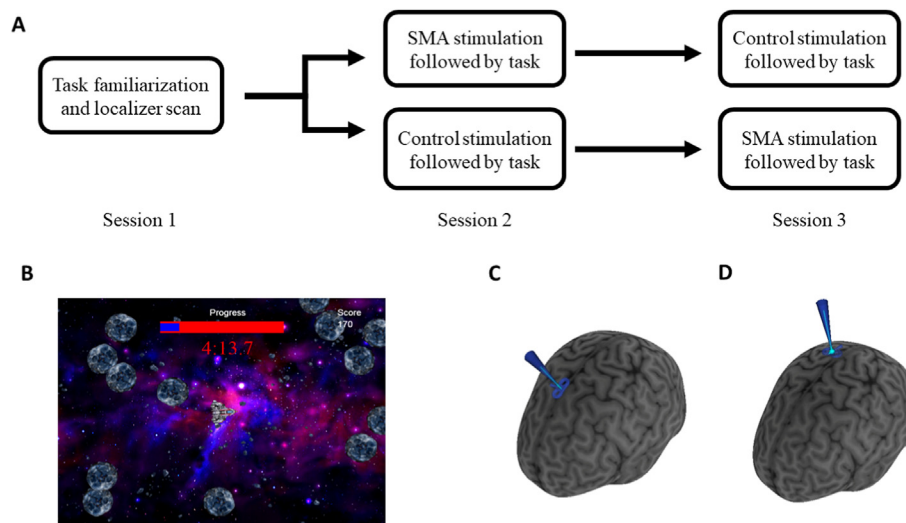


Fig. 1 – An overview of the methods and design: **A**, the experimental design. Following the familiarization session, participants completed two stimulation sessions: SMA stimulation and control precuneus stimulation (counterbalanced) with at least one week apart. **B**, a sample screen from the spaceship task. The red bar represents the overall time of the block, whereas the blue bar represents the time passed since the beginning of the block. The timer (red numbers) counts the time left for the block. A white number at the top-right corner of the screen indicates the current score. **C**, Location of SMA stimulation site, and **D**, location of control precuneus stimulation site localized and maintained online using neuro-navigation.

the last session of the experiment. In the initial session prior to the localizer task, participants were familiarized with the spaceship task initially for a 5-min practice in which no bonus was awarded, and afterwards for a 10-min block identical to the ones in the experimental sessions.

Each spaceship task block was divided into seven equal time-segments. For each participant, we standardized the number of spacebar presses in each time-segment: we subtracted the number of spacebar presses in each segment from the condition mean, and divided the result by the standard deviation of that block. This resulted in a z-score for each segment within each block. To indicate a robust STIM effect, whereby the graph that plots effort as a function of time segment has a U-shape pattern, the vertex should be determined, along with two linear trends, a decreasing trend from the starting point to the vertex, and an increasing trend from the vertex to the end (Simonsohn, 2018). We thus report these linear trends as our main analyses. The Supplementary Online Materials (SOM) present an additional quadratic regression analyses. We first established the presence of the hypothesized U-shaped pattern, by plotting effort (standardized key-presses) as a function of time-segment in each condition separately and later tested whether the pattern differed between conditions. A behavioral pilot study with similar parameters (e.g., user interface, projectile range, length of training in the familiarization session; $n = 98$) showed the vertex to be at $\text{Time} = 3$, and demonstrated a significant STIM effect. The present experiment confirmed Segment 3 as the vertex (see below). Importantly, we chose keypresses as our dependent measure rather than actual scores because keypresses reflect attempts to score rather than actual success. For further validation of this measure, we found the Pearson correlations between scores and keypresses were .71, .72, and .86 in the SMA, precuneus and familiarization conditions, respectively. In addition, the number of spacebar presses correlated with factors that are known to affect motivation: It increases when the end-point was known versus unknown (Control Experiment 1), when action efficiency was made higher by long versus short range of shots, with large versus low number of asteroids on the screen, and when opportunity cost decreased (Emanuel, Katzir & Liberman, in prep). Statistical analyses of behavioral and self-report data were conducted via the R program (version 3.6.0) and the lme4, BayesFactor, piecewiseSEM, lsr packages. R syntax, digital materials (including the PANAS questionnaire and the localizer raw individual data), and data for the main analyses are available at <https://bit.ly/2KtbSbn>.

2.3.1. Self-report measures

In each session, participants completed the following measures: (1) subjective performance questionnaire, which consisted of two items (“I felt my performance was good during the task”; 0 - *totally disagree*; 11- *totally agree*; “I was effective in controlling the spaceship, shooting asteroids, etc.”; 0 - *totally disagree*; 11- *totally agree*; $\alpha = .96$), (2) a PANAS questionnaire asking participants to report their affective state *at the moment* and (3) a PANAS questionnaire asking participants to report their affective state *during the spaceship game*. Items were presented in a randomized order. The PANAS questionnaire has three indices: positive affect (e.g., “proud”), negative affect

(e.g., “upset”), and arousal (e.g., “alert”). One item was omitted from the PANAS questionnaire regarding negative affect *during the spaceship task* due to a programming error. Reliability measures for all PANAS subscales ranged between $\alpha = .85$ and $\alpha = .91$. These measures were included to explore the question whether SMA stimulation would affect self-reported level of performance and affect.

2.4. Imaging data acquisition

During a functional MRI scan, participants repeatedly tapped with their non-dominant (left) hand a sequence of two-finger movements (i.e., index and middle finger; “1-1-1-1, 2-2-2-2, 3-3-3-3, 4-4-4-4”) as quickly and accurately as possible for 10 s, followed by a 10 s interval. In other words, participants tapped on the keyboard repeatedly for four times for each presented digit, using their index and middle fingers of the left hand. The left hand was used in the localizer because participants pressed the spacebar with their left hand during the experimental task itself. The left hand is commonly used to avoid potential ceiling effects that often emerge when participants use their dominant (typically right) hand. The sequence was repeated nine times for 190 s. Each key press produced a dot on the screen, and the entire sequence of dots was displayed on a monitor to the subject. Because the SMA is known to be recruited in motor tasks of this sort (Boecker et al., 1994; Erdler et al., 2000; Lang et al., 1990), we sought to utilize a simple motor task that can be performed inside the scanner in a simple block-design, and providing a robust localizer due to a large number of measurements in a relatively short period. Prior to the fMRI scan, we introduced participants with the task outside of the scanner, and made sure they understood the experimental instructions by asking them to perform the task for 90 sec.

Imaging data were acquired with a 3 T SIEMENS MAGNETOM Prisma scanner equipped with a 20-channel head coil at the Alfredo Federico Strauss Center for Computational Neuroimaging, Tel Aviv University. Structural images were acquired with an MPRAGE sequence (repetition time/echo time [TR/TE] = 1750/2.61 msec; flip angle = 8; field of view [FOV] = 224 × 224 mm; slice thickness = 1 mm; 176 axial slices). Localizer fMRI scans were acquired with a gradient echo-planar imaging (EPI) sequence of functional T2*-weighted images (TR/TE = 2000/30 msec; flip angle = 82; FOV = 208 × 208 mm; slice thickness = 2 mm; 66 interleaved axial slices per volume). The functional scans comprised a total of 95 volumes and lasted 190 sec.

2.5. Imaging data analysis

Raw imaging data in DICOM format were converted to NIFTI format and preprocessed through a standard preprocessing pipeline using the FSL package version 5 (S. M. Smith et al., 2004). Functional image time series were first aligned using the MCFLIRT tool to obtain six motion parameters that correspond to the x-y-z translation and rotation of the brain over time. The skull was removed from the T2* images and from the T1 images using the brain extraction tool (BET; see SOM). Spatial smoothing was performed using a Gaussian kernel with a full-width half maximum (FWHM) of 5 mm. Data

and design matrix were highpass filtered using a Gaussian-weighted least-squares straight line fit with a cutoff period of 100 sec. Grand-mean intensity normalization of each run's entire four-dimensional data set by a single multiplicative factor was also performed. The functional volumes for each participant were registered to the high resolution T1-weighted structural volume using a boundary-based registration method implemented in FSL5 (BBR; Greve & Fischl, 2009). We included the six motion realignment parameters obtained from MCFLIRT, and framewise displacement (FD) as confound regressors.

A General Linear Model (GLM) analysis was performed on the motor localizer task data in a blocked design, which included regressors for the onsets of each trial. We included the six motion regressors and framewise displacement (FD) described above, as confound regressors. We contrasted the active trials, in which participants tapped their fingers repeatedly, against the baseline trials, in which participants were instructed to rest. The trial onset regressors were convolved with a canonical double-gamma hemodynamic response function. The temporal derivative of each regressor was included in the model. The model was estimated separately for each participant. z-statistic images were thresholded non-parametrically using clusters determined by $z > 3.1$ (using a cluster-based Gaussian random field correction for multiple comparisons) and a cluster significance threshold of $p = .05$ (Jezard et al., 2001).

2.6. Noninvasive brain stimulation

On each of the two experimental sessions, the spaceship task was performed immediately following application of a common inhibitory rTMS protocol at 1 Hz for 15 min (Censor et al., 2014; Dayan et al., 2018; Robertson et al., 2001) via a figure-of-eight coil (AirFilm -Rapid version, Magstim, Whitland, United-Kingdom, www.magstim.com), delivered to either SMA or the precuneus as a control site (Zénon et al., 2015). The site of the SMA stimulation was individually defined as the peak voxel of SMA identified from the fMRI localizer scans, which was validated to correspond anatomically to the SMA (Bozkurt et al., 2016), and then normalized to MNI space. The SMA stimulation site of one participant was defined anatomically due to unreliable localizer activation patterns. The control site was localized using the control site coordinates used by Zénon et al. (2015), adjusted anatomically within the precuneus boundaries of each subject. Specifically, the target precuneus site was set to be within the area posterior to the postcentral sulcus, and anterior to the parieto-occipital sulcus (Bruner et al., 2014). The mean rTMS location coordinates were 4.04 ± 1.37 , -13.11 ± 6.36 and 59.78 ± 4.93 (x, y, and z $\pm$ SD) for the SMA (Figs. 1D), and 6.95 ± 1.04 , -52.72 ± 26.53 and 65.54 ± 3.83 for the precuneus (Fig. 1D). The site was marked on each subject's T1-weighted anatomical image using a neuro-navigation system (Brainsight 2, Rogue Research, Montreal, Canada, www.rogue-research.com). In addition, the neuro-navigation system was used to coregister participants' heads and to mark stimulation sites prior to rTMS administration. Six landmarks were used for coregistering the participant's head to their MRI anatomic scan (nasion, tip of the nose, left and right crus of helix and left and right cymba). The coil was

positioned at a 90° angle for SMA stimulation and at 0° angle for the precuneus stimulation.

The resting motor threshold (RMT) was defined as the minimal right primary motor cortex (M1) stimulation intensity yielding 5 out of 10 motor-evoked potentials (MEPs) greater than .05 mV in the left first dorsal interosseous (FDI) muscle (Rossini et al., 1994). M1 mean stimulation coordinates were 39.90 ± 4.50 , -26.07 ± 5.17 and 58.92 ± 6.11 . Then, rTMS stimulation was given at 120% of RMT for 15 min, at a frequency of 1 Hz, known to induce an inhibitory effect on cortical excitability of the targeted area (Chen et al., 1997; Sandrini et al., 2011). This corresponded to $67.56 \pm 12.48\%$ (mean $\pm$ SD) of the 2 T maximum stimulator output.

3. Results

3.1. Confirming the vertex of the effort distribution pattern

We expected both conditions to exhibit a STIM pattern of effort distribution in the course of the task, which is essentially a U-shape dependency of level of effort on time. After an initial inspection of this dependency, which confirmed a U shape (Fig. 2, see also formal analyses below) we sought to determine the vertex of the STIM pattern. Specifically, as the pretest identified the vertex at Time-Segment 3, we sought to further validate this segment as the vertex also in the present experiment. To that end, we identified for each participant in each condition the segment with the minimum keypresses. We found this segment to be 3 in the SMA condition ($Mdn_{SMA} = 3$, $M_{SMA} = 2.94$, $SD_{SMA} = 1.73$), and 3.5 in the control condition ($Mdn_{control} = 3.5$, $M_{control} = 3.5$, $SD_{control} = 1.91$), and therefore proceeded with analyses of interrupted regression using Segment 3 as the vertex.

3.2. Stuck-in-the-middle

We tested for a U-shape separately in each condition by fitting an interrupted regression model to each condition, nested within participants (see Equation (1); Marsh & Cormier, 2001, p. 7). This model tested for two linear trends (1) from the starting point to the vertex (i.e., from the 1st time segment to the 3rd time segment): and, (2) from the vertex to the end (i.e., from the 3rd time segment to the 7th time segment). A significant negative slope for (1) and a significant positive slope for (2) would indicate a U-shaped dependency of spacebar presses on time, akin to the STIM pattern. The analysis was done by coding three dummy variables (Marsh & Cormier, 2001; Muggeo, 2003; Simonsohn, 2018): A dummy variable indicating the downward trend, $time_{downward} = time - turning$ point if $time \leq turning$ point and 0 otherwise; a dummy variable indicating the upward trend, $time_{upward} = time - vertex$ if $time \geq vertex$ and 0 otherwise; and a dummy variable controlling for the intercept at the vertex, $upward = 1$ if $time \geq vertex$ and 0 otherwise. In this and all subsequent multi-level analyses, we followed Bliese and Ployhart's (2002) recommendations for adding random effects based on the deviance index for goodness of fit. Based on this criterion, we included in our model random slopes for the downward and

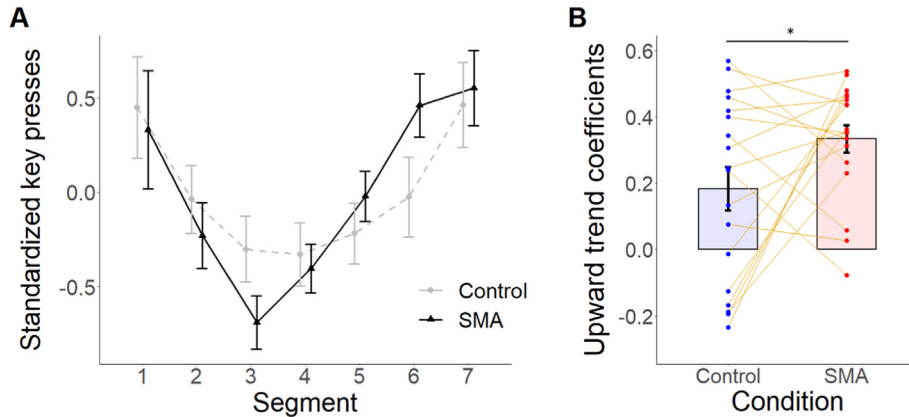


Fig. 2 – Effects of stimulation on distribution of effort over time: A, mean standardized spacebar presses per segment by condition. The black and dashed gray lines represent performance following SMA and control rTMS, respectively. B, Mean coefficients for the upward trend (segments three to seven) by condition. Error bars represents SEM across participants. * $p < .05$.

upward trends. The models' fixed effects specifications were of the following form:

$$Y_{time(j)} = b_0 + b_1 * Time_{downward(j)} + b_2 * Time_{upward(j)} + b_3 * Upward_j \quad (1)$$

$Y_{time(j)}$ is the z-score of spacebar presses in time segment j , b_0 is the intercept, b_1 and b_2 are the coefficients of the linear downward and upward trends of time, respectively. The b_3 coefficient controls for the intercept of the upward trend (adding this coefficient for statistical analyses of U-shapes is recommended by [Simonsohn, 2018](#). This coefficient makes the model an interrupted rather than a segmented regression model, e.g., [Muggeo, 2003](#)).

In the SMA condition, significant slopes were found for both the downward ($b_1 = -.559$, $SE = .246$, $t(53.80) = -2.75$, $p = .027$, 95% CI $[-1.04, -.115]$), and upward ($b_2 = .334$, $SE = .066$, $t(18.01) = 5.02$, $p < .001$, 95% CI $[.201, .471]$) trends, which indicated a STIM effect. In the control condition, marginally significant slopes were found for both the downward ($b_1 = -.482$, $SE = .258$, $t(75.91) = -1.87$, $p = .064$, 95% CI $[-.985, .061]$), and upward ($b_2 = .182$, $SE = .091$, $t(17.74) = 1.98$, $p = .062$, 95% CI $[.009, .364]$) trends, also indicating a STIM effect.

In order to examine the differences between conditions, we added to the model specified in Equation (1) a dummy variable representing condition (control condition was coded as Condition = 0), and two interaction terms (see Equation (2)) – one tested for difference between conditions in the downward trend from the first point to the vertex, and the other tested for difference between conditions in the upward trend, from the vertex to the last point. Both were nested within participants. The model included a random intercept, and random slopes for downward and upward trends. The models' fixed effects specifications were of the following form:

$$Y_{time(j)} = b_0 + b_1 * Time_{downward(j)} + b_2 * Time_{upward(j)} + b_3 * Upward_j + b_4 * Condition + b_5 * Condition * Time_{downward(j)} + b_6 * Condition * Time_{upward(j)} \quad (2)$$

$Y_{time(j)}$ is the z-score of spacebar presses in time segment j , b_0 is the intercept, and b_1 and b_2 are the coefficients of the linear downward and upward trends of time in the control condition, respectively. Also, b_4 is the coefficient of the difference between the two conditions at a centered value of $Time_j$. In addition, b_5 and b_6 are the coefficients of the downward and upward trend interaction of time with condition, respectively.

Condition did not interact with the downward trend ($b_5 = -.060$, $SE = .147$, $t(210.97) = -.411$, $p = .681$, 95% CI $[-.343, .213]$), but condition did interact with the upward trend ($b_6 = .152$, $SE = .071$, $t(210.97) = 2.12$, $p = .034$, 95% CI $[.010, .292]$), which indicated a steeper increase in effort in the SMA condition than in the control, precuneus condition.

In order to further validate the precuneus as a control site, we conducted the same analyses as presented in Equation (2), comparing each of the SMA and control conditions to the 10-mins block from the familiarization session, in which no stimulation was administered prior to the spaceship task. When comparing the SMA and the familiarization conditions, a time by condition interaction ($b_6 = .25$, $SE = .067$, $t(210.97) = 3.80$, $p < .001$, 95% CI $[.127, .390]$) indicated a steeper increase in effort towards the end of the block in the SMA condition than in the familiarization condition. When comparing the precuneus and the familiarization conditions, no time by condition interaction ($b_6 = .10$, $SE = .077$, $t(211.02) = 1.32$, $p = .188$, 95% CI $[-.052, .257]$) was found. Thus, the SMA condition exhibited a steeper, more pronounced STIM pattern not only in comparison to the precuneus condition, but also in comparison to the familiarization, no-TMS condition. Furthermore, the finding that the precuneus condition did not significantly differ from the familiarization condition supports using it as a control site.

3.3. Control analysis, overall effort

We examined the difference in the overall rate of spacebar presses between the two experimental conditions (Fig. 3), and found no significant difference ($M_{SMA} = 4.19$, $SD_{SMA} = .66$,

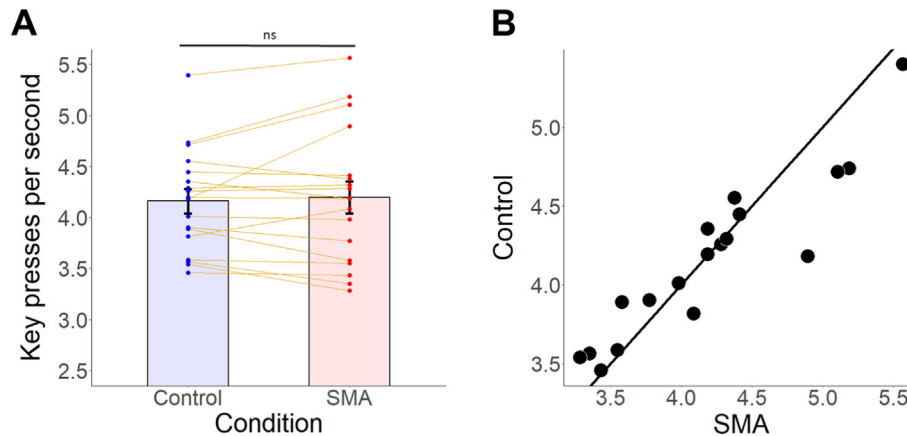


Fig. 3 – Control analysis, overall effort across conditions: A, overall effort (key presses per second) following SMA and control stimulation. Orange lines represent single subject data. Error bars represent standard error of the mean. B, overall effort following SMA and control stimulation was highly correlated between conditions, an identity line was added to this figure.

$M_{\text{control}} = 4.16$, $SD_{\text{control}} = .50$; paired-sample t -test, $t(17) = .58$, $p = .565$, $d = .13$). A Bayesian t -test (Morey et al., 2015; $r_{\text{prior}} = .707$) indicated that the data were 3.53 times more likely to occur under a model of zero difference between the two conditions ($BF_{01} = 3.53$; Jarosz & Wiley, 2014, p. 490) than under a model of a non-zero difference. Moreover, the rate of spacebar presses in the two conditions was highly correlated across participants, $r(16) = .92$, $p < .001$. This result is in line with Zénon et al. (2015), who did not find any effect of SMA stimulation on overall effort exertion in grip force.

3.4. Self-report measures

We examined the difference in each of the self-report indices between the two experimental conditions in a paired-sample t -test. No significant differences were found. Bayesian t -tests indicated that a null model was more likely in all measures (BF s ranges between 2.54 and 4.04).

3.5. Control experiments

We conducted three control experiments in order to confirm the validity of the parameters chosen in the main experimental paradigm, and to ensure a reliable STIM effect. Namely, a STIM is expected to occur when a clear end-point is available, and during prolonged tasks. A first control experiment showed that a STIM pattern of effort allocation emerged only when the elapsed game-time was shown on the screen (a timer at the top of the screen indicated the time left), whereas the STIM pattern was absent when no timer was shown. In Control Experiments 2 and 3, a STIM pattern was found when the task was relatively long but not when it was relatively short (in both experiments, participants were informed about the existence of both experimental conditions). Experiment 2 examined this effect when participants had to achieve a target score, and Experiment 3 examined the same effect when participants worked toward a deadline. These experiments verified that the STIM pattern requires prolonged tasks with a deadline, as performed in our main experimental design. We

analyzed the data in the same way as in the main experiment. These experiments are reported in full in the SOM. A preregistration of Experiment 3 is available via <https://aspredicted.org/7vb5m.pdf>.

4. Discussion

We investigated the neural mechanisms underlying patterns of effort allocation, and the “stuck-in-the-middle” (STIM) effect specifically, whereby humans invest effort at the beginning and the end of prolonged tasks, yet reduce effort in the middle. Effort distribution was measured following inhibitory rTMS over the SMA or a control site. The results showed that inhibitory SMA stimulation resulted in a more pronounced STIM effect compared to control stimulation. In addition, a control analysis showed that consistent with previous findings (Zénon et al., 2015), similar levels of effort were found in both conditions.

Extant explanations of the STIM pattern of effort allocation suggest that it is caused by an increase in perceived reward per unit of effort near the starting- and end-points of a task (Bonezzi et al., 2011; Cryder et al., 2013; Heath et al., 1999; Koo & Fishbach, 2012). This is because effort is perceived as more rewarding the more impact it is perceived to have on goal progress. Impact, in turn, is perceived as higher near the starting and end-points of a task. For example, the 6th step out of a 10-step path closes 20% of the remaining path, whereas the 9th step closes 50% of the remaining path. Similarly, the 2nd step on this path increases distance from the starting point by 50%, whereas the 5th step increases it only by 20%.

Changes in opportunity-cost may also contribute to a STIM pattern of effort allocation. Kurzban et al. (2013) suggested that opportunity-cost of engaging in any activity (e.g., attentional focus, working memory engagement etc.) increases in its course. For example, people tend to get increasingly bored as they continue working on a task, and their desire to do something else increases. Independently and in addition to this effect, closer to the end of any task, opportunity-cost of

engaging in any activity reduces simply because other activities are being put off for a shorter time. For example, if only one minute remains for a focal task, postponing mind-wandering or adjusting one's seat until its end is less costly than when 10-mins remain. Together, these two processes give rise to relatively low levels of opportunity-cost close to the beginning and the end of a task, and high levels of opportunity-cost in the middle. In the present experiment, we hypothesized that stimulation to the SMA would make participants process effort as less costly (as in Zènon et al., 2015), which would, in turn, make them engage less in strategic planning of effort, and be more responsive to local cues (how close one is to the beginning and the end of the task) that often alter the level of invested effort. Accordingly, this should give rise to a steeper STIM pattern.

In sum, extant literature explains the STIM pattern as being the result of moment-to-moment changes in (perceived) effort-reward and effort-cost. Our results, which showed that SMA inhibition accentuated the STIM pattern, suggest that SMA inhibition sensitized participants to such local changes. In other words, our results suggest that the SMA might be involved in producing a flatter distribution of effort in the course of an extended task, which is less sensitive to moment-to-moment changes in effort-cost and effort-reward. These results are consistent with previous theorizing about the role of the SMA in processing task-demands.

It is important to consider motor inhibition as an alternative explanation for the obtained pattern of results. Specifically, a disruption of SMA activity might have reduced participants' fine motor performance and control (e.g., Schramm et al., 2019), giving rise to a steeper reduction in spacebar presses as the task continued. While this remains an important alternative to keep in mind, we think that some aspects of our results make it less likely. Specifically, we find no difference in overall spacebar presses between the SMA and the precuneus conditions, which suggests no difference in overall effort between the two conditions. Possibly, pressing the spacebar through the game did not require a high level of fine motor control, leaving effort-measurement unaffected.

The SMA has been implicated in the coding of effort cost during both actual effort exertion (De Morree et al., 2012) and anticipated effort-exertion (Bonnelle et al., 2015; Burke et al., 2013; Croxson et al., 2009). Croxson et al. (2009) manipulated effort by altering the number of times participants had to move a cursor to a target location on a computer screen via a trackball mouse (e.g., three times for low-effort, and 15 times for high-effort). They found an increased blood-oxygen-level-dependent (BOLD) signal in the SMA when participants were presented with a cue that indicated an upcoming change in level of effort. Burke et al. (2013) found a higher increase in BOLD signal in the SMA in response to cues that indicated an upcoming high-effort task (producing 75% or 100% of maximal grip force) compared to a low-effort task (no grip or 25% of their maximal grip-force).

Most relevant to our study and as described earlier, inhibition of the SMA has been found to reduce perceived cost of effort (Zènon et al., 2015), without affecting actual invested effort as measured by handgrip strength. Our results are consistent with these findings. In our experiment, too, inhibition of the SMA did not affect overall level of invested effort,

and only made effort allocation over time less evenly, presumably due to increasing sensitivity to local, moment-to-moment changes in effort-cost and effort-reward.

An important distinction has to be emphasized between reward for effort and reward for goal completion (Inzlicht et al., 2018). Effort reward in goal-pursuit is the amount of progress per unit of effort, and is not dependent on the value of reaching the goal (Karsh et al., 2016). For example, whether one's goal is to raise \$100,000 for an important or a less important purpose, raising the last \$1000 closes 100% of the gap to the goal and should be more rewarding than raising the 20th \$1000. As another example, keeping the final outcome constant, effort is more rewarding when progress is more conspicuous and when one has a stronger sense of contingency between the effort one invests and the progress that it produces (Liberman & Dar, 2009). Most importantly for the present framework, effort reward changes in the course of the task even when reward for goal completion remains the same. Our results raise the possibility that the SMA is involved in regulating effort in the course of a task (making it more evenly distributed and less sensitive to moment-to-moment changes in effort-reward and effort-cost) but they do not speak to its role in regulation of behavior according to the reward of a goal.

The SMA relates to other brain regions which are also involved in evaluating goals and choosing to initiate activities (Nachev et al., 2008). For example, Bonnelle et al. (2015) found that higher functional connectivity between the SMA and the dACC was associated with a lower level of behavioral apathy, which is a general tendency to avoid task initiation. In a similar vein, Shenhav, et al. (2013; see also Kolling et al., 2016; Shenhav et al., 2017) have suggested that the dACC is involved in determining overall intensity of effort and in choosing which tasks to engage. In support of this notion, dACC activity was recently found to monitor real-time conflict, for possible use in on-line action control (Smith et al., 2019). Other studies have also suggested that the midcingulate cortex (MCC) is involved in determining the way actions are deployed or altered based on the value of the relevant goals (Shackman et al., 2011; Vogt, 2016). Future studies should examine the role of the dACC and MCC and their functional connectivity with the SMA in patterns of effort allocation in a course of a task.

Notably, the study design has possible limitations. First, it is possible that our control stimulation region, the precuneus, is in itself involved in effort allocation over time, as it was previously found to be implicated in meta-cognition and was negatively associated with anticipation (Desender et al., 2016; Rzepa et al., 2017). Accordingly, an inhibitory stimulation to this region might have caused participants to exhibit a shallower STIM pattern due to certain impairments in meta-cognitive capabilities related to strategic effort-allocation. In order to rule out this confound, we compared the STIM in the no-stimulation session with the STIM in the SMA session. This comparison replicated the difference in the upward trend between the SMA and precuneus conditions. Nevertheless, future studies might benefit from studying how disruption of the precuneus affects effort allocation over time.

The SMA has been shown to play a crucial role in space representation and domain-general sequence processes

(Cona & Scarpazza, 2019; Cona & Semenza, 2017), which might also be involved in the spaceship task used in our study. Accordingly, the SMA stimulation may have modulated the resources allocated for these processes rather than sensitivity to effort costs and rewards. It is possible, however, to see this process as compatible with our interpretation, if it mediated the effect of SMA stimulation on sensitivity to reward or cost cues. For example, it is possible that disruption of the SMA lowered the resources allocated to space-representation, making the effort exerted post SMA-stimulation seem less demanding/costly.

A better understanding of the mechanisms of effort allocation over time and the STIM pattern in particular can hold important practical implications, as it would afford changing this pattern, whenever such change is deemed desirable. For example, the STIM pattern is observed in top athletic performances (e.g., among world-record track runners, Tucker et al., 2006; Emanuel, 2019), and is more pronounced in important competitions (e.g., in finals as compared to heats in Olympic rowing; Muehlbauer et al., 2010) and among medalists as compared to non-winning competitors (e.g., increase in velocity near the end of an open-water swimming world championship; Veiga et al., 2019). If a STIM pattern of effort allocation is indeed conducive to top athletic performance, then understanding its neural and behavioral causes holds the promise to help athletes achieve better results. Importantly, in other situations the STIM pattern of effort allocation might be detrimental to overall performance. For example, it is not necessarily optimal for students to work hard in the beginning of the semester and towards the exams and slack in the middle. In these cases, too, a better understanding of the causes of the STIM pattern can help overcome such tendencies.

Credit author statement

A.E., J.H., H.S., N.L. and N.C. designed research and experimental protocol; A.E. and J.H. performed research; A.E. analyzed data; A.E., N.L., J.H. and N.C. wrote and edited the manuscript.

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Open practices

The study in this article earned Open Materials, Open Data and Preregistered badges for transparent practices. Materials and data for the study are available at <https://bit.ly/2KtbSbn>.

Declaration of competing interest

The authors declare no competing financial interests.

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cortex.2020.10.018>.

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