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Noise in the brain: Transcranial random noise stimulation and perceptual noise act on a stochastic resonance-like mechanism

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Abstract

Stochastic resonance (SR) is a phenomenon in which a certain amount of random noise added to a weak subthreshold stimulus can enhance signal detectability. It is unknown how external noise interacts with neural noise in producing an SR-like phenomenon and whether this interaction results in a modulation of either network efficiency or the efficiency of single neurons. Using random dot motion stimuli and noninvasive brain stimulation, we attempted to unveil the specific mechanism of action of the SR-like phenomenon in motion perception, if present. We aimed to determine whether signal integration efficiency changes with external noise (random dot numerosity) and how electrical transcranial random noise stimulation (tRNS) can affect the peak performance. The participants performed a coherent motion detection task in which the random dot numerosity varied, whereas the signal-to-noise ratio (SNR) remained constant. We applied placebo or tRNS with an amplitude of either 1 or 2 mA during task execution. We found peaks in participants' performance both in the case of placebo stimulation and in the case of 1-mA tRNS. In the latter case (i.e., with an additional noise source), the peak emerged at lower random dot numerosity levels than when no additional noise was added (placebo). No clear peak was observed with 2-mA tRNS. An equivalent noise (EN) analysis confirmed that SR arises from a modulation of the network efficiency underlying motion signal integration. These results indicate a joint contribution of external and neural noise (modulated by tRNS) in eliciting an SR-like phenomenon.

KEYWORDS
equivalent noise, coherent motion, noise, stochastic resonance, tRNS

1 | INTRODUCTION

Noise, in a nutshell, is something that interferes with our ability to perceive or process information; therefore, it is considered to be something undesirable that can have only negative effects. However, although counterintuitive, it is well established that in some specific cases, noise can enhance sensitivity and therefore information processing. This phenomenon, known as stochastic resonance (SR), can play a functional role in the brain. For example, a proper amount of noise added to a visual (Simonotto et al., 1997; Ward et al., 2002), tactile (Collins et al., 1995; 1996) or auditory (Zeng et al., 2000) subthreshold signal may enhance signal detectability, rather than decreasing it. Generally, noise modulates the detection of sensory signals according to an inverted accuracy × noise U-shaped function, which commonly describes the SR phenomenon.

In vision, an SR-like phenomenon was first described by Simonotto et al. (1997). They presented images comprising a set of strips obtained by sinusoidally varying gray levels (gratings). The contrast remained at threshold throughout the experiment, whereas the level of noise varied randomly. The results showed that an appropriate amount of noise led to improvements in contrast detection. Studies following that one have further explored how the SR-like phenomenon affects contrast sensitivity (Blackwell, 1998; Goris et al., 2008; Sasaki et al., 2006; van der Groen et al., 2018; van der Groen & Wenderoth, 2016) as well as how it affects the perception of visual stimuli involving high-level visual processing, such as that of ambiguous figures (Leopold et al., 2002), three-dimensional shapes (Ditzinger et al., 2000) and global motion embedded in random dot motion (Pavan et al., 2019; Treviño et al., 2016).

Most studies have focused on the relationship between sensory performance and the amount of external noise (i.e., external variables—perceptual stimuli with no relevance to the task). However, other studies have suggested that SR can also be internally induced (Aihara et al., 2010). In this manuscript, we define *neural noise* as the noise that arises at the nervous system level and consists of noisy/random fluctuations in brain activity (Faisal et al., 2008). It can be, for example, a consequence of the probabilistic nature of ion channel gating and synaptic transmission (Faisal et al., 2008). These events result in increased variability and, theoretically, could interfere with behavioural performance, although some studies have suggested that neural noise could be beneficial also (Douglass et al., 1993).

Neural noise can be increased through electrical transcranial random noise stimulation (tRNS), a form of alternate current with random frequency (Fertonani & Miniussi, 2017; Miniussi et al., 2013). Van der Groen and Wenderoth (2016) found that tRNS over the occipital cortex enhanced visual performance in an SR-like manner, as does external visual noise. They showed that administrating 1-mA tRNS to the occipital cortex increased the detection of Gabors, whereas detection decreased with lower and higher intensities, demonstrating the inverted U-shaped function typical of SR.

In a recent study, Pavan et al. (2019) used a similar stimulation design to that used by van der Groen and Wenderoth (2016) but with a task involving global coherent motion (CM) discrimination.[1] The results supported the hypothesis that adding neural noise through tRNS induces effects compatible with the SR phenomenon.

To corroborate their hypothesis, Pavan et al. (2019) performed an equivalent noise (EN) analysis (see also Dakin et al., 2005; Ghin et al., 2018) aimed at exploring the source of the SR-like effect induced by tRNS. The EN model assumes that the visual system randomly samples a given number of dots among the total number of dots and that a correct response is provided when at least one of these sampled dots is a CM dot. The EN analysis results led the authors to suggest that compared with the control (i.e., placebo) condition, 1.5-mA tRNS improved CM discrimination by increasing the number of dots that the visual system sampled rather than affecting the precision with which the direction of each dot's movement could be estimated (the authors labeled the factors that affect the direction of each dot's movement as local noise). Based on these results, Pavan et al. (2019) concluded that the tRNS-induced SR-like effect emerges because of increased motion signal integration—that is, increased efficiency with which local motion directions are pooled together by the visual system.

When considering the pooling response underlying global motion integration, the crucial variable is the number of detectors that are pooled by high-order motion integration mechanisms (Britten et al., 1992; Dakin et al., 2005). At a behavioural level, an increase in the number of pooled detectors can be achieved through an increase in the number of coherent dots in the visual stimulus (Britten et al., 1992). If the number of noncoherent dots is fixed, the signal-to-noise ratio (SNR) increases (Britten et al., 1992); if instead the number of noncoherent dots is increased proportionally, the SNR remains constant (Dakin et al., 2005). In the latter case, there is a proportional increase of signal and external noise. An

[1] CM is usually obtained by presenting a field of small moving dots, some of which coherently move in the same direction and the rest of which move randomly. Dots carrying specific motion signals are correlated in both space and time. They are replotted with a fixed spatial offset after a fixed temporal interval, generating a global motion percept.

SR-like phenomenon would mean that up to a certain level of external noise, there would be an increase in the number of detectors pooled together (integrative mechanisms) and, consequently, an increase in signal detection performance. Beyond that level, the signal would be masked by an excessive amount of noise, and performance would deteriorate. Using a CM detection task, our first experiment confirmed this prediction: Performance increased as a function of dots numerosity up to a certain level (peak) and then decreased.

A second question was how tRNS could modulate integrative mechanisms. Increasing the level of neural noise (Aihara et al., 2008; Kitajo et al., 2007, 2003; Miniussi et al., 2013) is not always detrimental but in fact can be good for stimulus detection at (sub)threshold levels. According to Pavan et al. (2019), tRNS could enhance integrative mechanisms in global CM tasks. Our hypothesis is that neural noise and external noise can both exert influence on integrative mechanisms. If this hypothesis is correct, we would expect the amount of external noise required to achieve the performance peak to be smaller when the tRNS-induced neural noise is present than when the noise is not present. This is because in the former case, the external noise adds to the neural noise, so a smaller amount of external noise is necessary to achieve the peak performance. Thus, under the tRNS conditions, the performance peak should be associated with a smaller number of dots (external noise) than that with which it is associated in the sham (placebo) condition. However, Pavan et al. (2019) also showed that when the tRNS signal was too strong, integrative mechanisms' efficiency could decrease. Therefore, a relatively strong 2-mA tRNS may lead to poor performance at all dot numerosity levels. Our second experiment's results confirmed these predictions.

Finally, we conducted an EN analysis to confirm that external and neural noise actually modulate the visual system's sampling efficiency (motion integration mechanisms; Dakin et al., 2005; Pavan et al., 2019).

2 | METHODS

2.1 | Participants

Eighteen healthy individuals (11 females, age 26.9 ± 4.2 years [mean ± SD], age range 21–33 years) who were students or workers at the University of Padua voluntarily participated in the behavioural experiment, and 24 different healthy individuals (13 females, age 26 ± 3.2 years [mean ± SD], age range 21–31 years) participated in the tRNS experiment. All participants had either normal or corrected-to-normal vision and were naïve regarding the experiment's purpose. Each individual received the experimental material (monitor and task instructions). Before starting, all participants watched a brief demonstration of the stimuli and the task, and they practiced the task for less than 2 min. Each participant signed an informed consent form on the day of the experiment. After completing the experiment, all participants were informed about the study's aim. This study was approved by the Ethics Committee of the University of Padua (protocol n. 3058) and was conducted in accordance with the Declaration of Helsinki and electrical stimulation safety guidelines (Antal et al., 2017).

2.2 | Procedure

Each of the two main experiments (the behavioural and the first day of the tRNS experiments; see Figure 1) was preceded by a session of threshold assessment and a session of threshold verification. In all the sessions (i.e., threshold assessment, threshold verification and main experiments), the task was a two-interval forced choice (2IFC) in which observers had to indicate which of two images contained the target dots (rightwards CM). In all session blocks, the SNR was kept constant, except the threshold assessment, for which the CM level changed according to a Levitt single one-up one-down staircase (Levitt, 1971). The tRNS experiment was within subjects; each participant executed the CM detection task under three different conditions. Under the three conditions, three different stimulation protocols were applied—namely, 1-mA tRNS, 2-mA tRNS and sham tRNS. The three conditions were separated by at least 2 days for washout purposes. The order of stimulation conditions was counterbalanced among participants.

2.3 | Apparatus

The participants were positioned in a dimly lit room, seated 57 cm away from the display screen. Viewing was binocular, and the visual stimuli were generated with MATLAB (R2016a) Psychtoolbox (Brainard, 1997; Pelli, 1997) and displayed on an LCD ASUS monitor (model ML228, version ML228H) with a refresh rate of 60 Hz (display size: 19 in.; resolution: 1920 × 1080 pixels; background luminance: .7 cd/m^2). Each pixel subtended approximately 1.5 arcminutes. The use of a chinrest ensured that the head remained at a fixed distance from the screen.

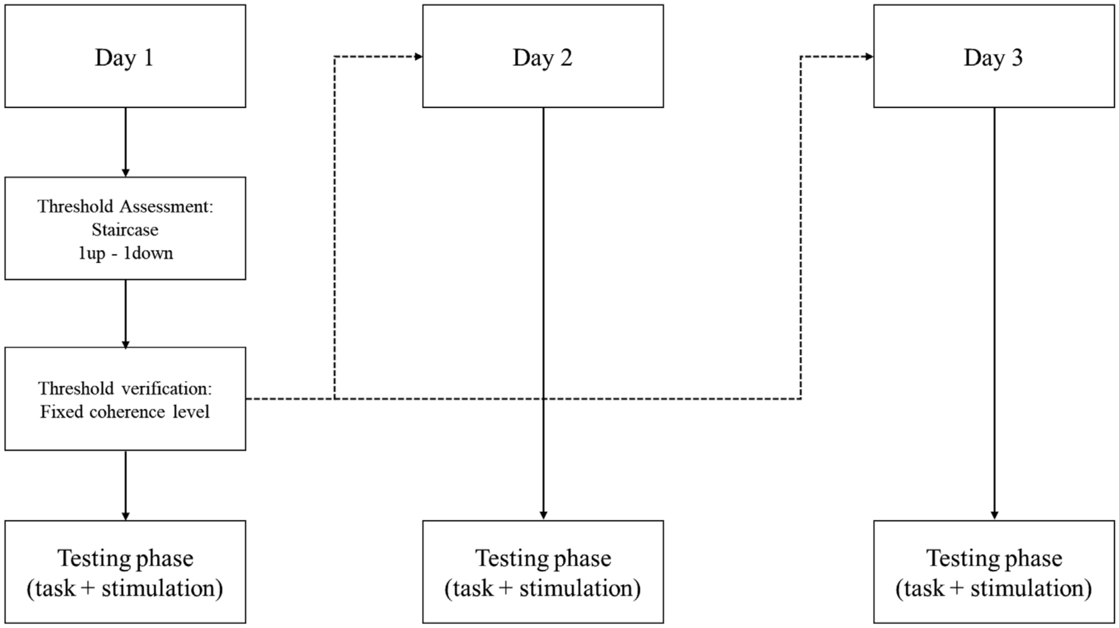


FIGURE 1 Outline of the study. Each participant executed the main task, that is, test + stimulation (1 mA, 2 mA, sham) three times on three different days. On day 1, the main experiment was preceded by a session of threshold assessment and a session of threshold verification to verify that individual performance was at a (sub)threshold level. Once the individual (sub)threshold level was verified, it was kept fixed on days 2 and 3.

2.4 | Stimulus and task

2.4.1 | CM

Each stimulus was a square window of 7.5 deg, filled in with white moving dots (.075 deg in diameter each). The motion sequence was computed as follows: On the first frame, the dots were randomly positioned within the square window and then displaced by .05 deg on each subsequent frame (Brownian motion; see Battaglini et al., 2017; Pilly & Seitz, 2009), producing a speed of 3 deg/s. Each stimulus consisted of an 8-frame motion sequence (i.e., 133 ms; each frame was 16.67 ms) displayed at the centre of the screen. Additionally, moving dots that travelled outside the window were replaced by new dots at different random locations within the square window; thus, the same density was always maintained. Random dot numerosity levels corresponded to the various levels of noise added to the target signal. The target stimulus was rightward CM, whereas the random moving dots constituted a field of moving dots with no coherent direction (Figure 2).

2.4.2 | Task description—CM detection task

Each trial comprised the random presentation of two intervals. One interval showed the CM, in which few target dots moved rightward among a field of randomly moving dots (target stimulus), and the other showed the randomly moving dots pattern. The participants were asked to recognize whether the target (CM) was presented during the first interval or the second interval by pressing the appropriate button on the keyboard. The second interval followed the first after 870 ms, and this timing was kept the same in all the experimental sessions. When the second stimulus disappeared, the participants made a decision and answered. The following trial started a second later, after the response was recorded. As already mentioned, the task was the same for threshold assessment, threshold verification and the two main experiments.

2.4.3 | Assessment of baseline performance: Threshold assessment and verification

The threshold value was assessed through a Levitt single one-up one-down staircase (Levitt, 1971). Each individual performed the CM detection task with 100 dots, but the amount of coherently moving dots within the target changed according to participants' responses. The first coherence level was set at 90% for every individual, and the step size was set at 10% so that the level of coherence decreased by 10% after the first right answer and increased by the same amount after the first wrong

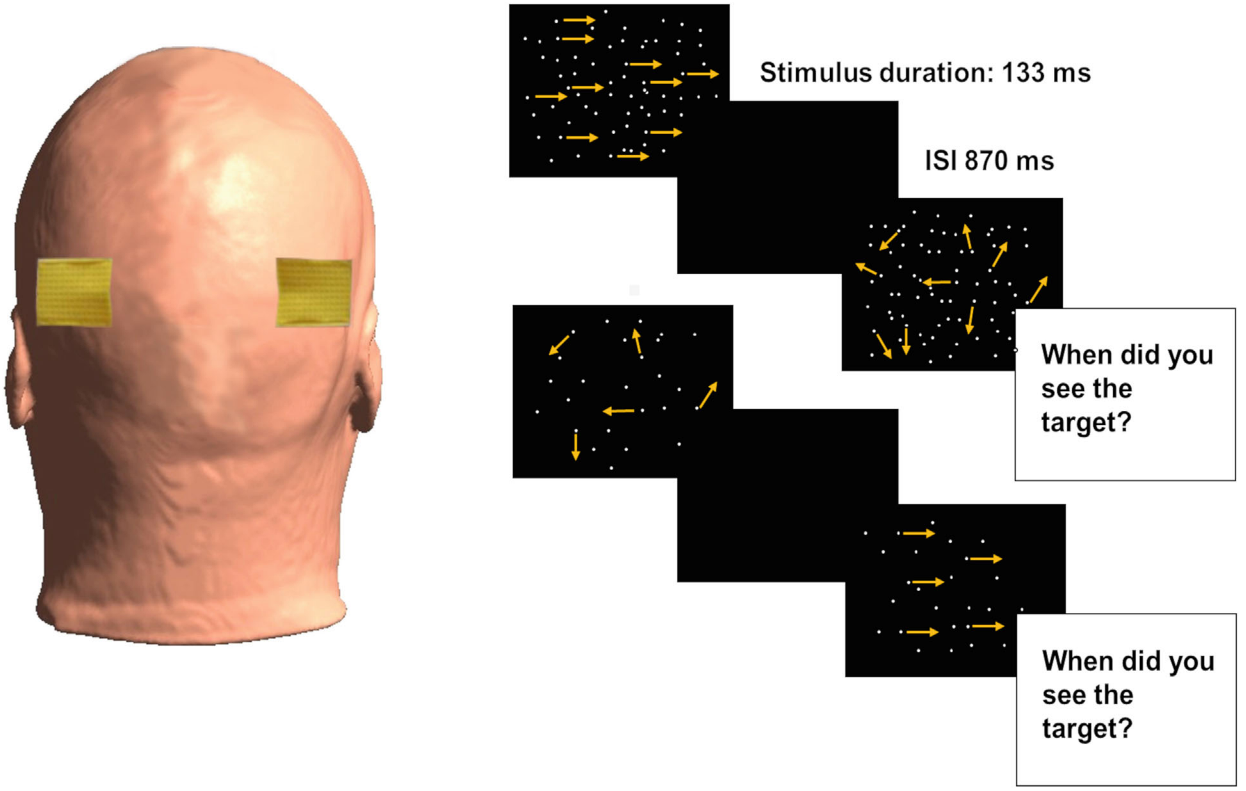


FIGURE 2 The left part of the figure represents the electrodes' positioning (for illustration purposes only; the electrodes' size in relation to the head's size is imprecise). The right part of the figure represents the experimental stimulus (coherent motion) with high (up) and low (down) dot numerosity. Black squares filled with dots represent the dot patterns, which displayed CM (target) or random movements in two different intervals. The interstimulus interval was 870 ms. After the second interval, the participants were presented with an unlimited response window in which they indicated whether the target appeared in the first or second interval. The next trials started 1000 ms after the button press.

answer. The step size was halved at every reversal (either a correct response followed by an incorrect response or vice versa). At the first reversal, the step size became 5%; at the second, 2.5%; and so on, until a minimum change of 1 dot was reached. The staircase ended after either 13 reversals had occurred or the participant had completed 100 trials. Under a 2IFC protocol, this adaptive method allowed us to assess the minimum level of coherence required for the observer to detect a rightward motion at threshold level—namely, in 75% of trials. The procedure was repeated five times, and the threshold corresponded to the average of the five measurements. Then, a verification of the baseline performance occurred. During this session, participants were presented with the same 2IFC protocol and performed the same task as in the threshold assessment session. Neither the number of dots (100) nor the coherence level changed across trials, and accuracy was measured after 24 trials. If a coherence level produced 70% ± 5% of the correct responses, it was considered appropriate to use in the next main experiment. If not, we adjusted the coherence level until the optimal performance was reached and used that coherence level for the main experiment (about 70% of correct responses).[2] For the tRNS experiment, in which three stimulation conditions were administered on different days, the threshold assessment and threshold verification were conducted on the first day only.

2.4.4 | Main behavioural task—CM detection task with 14 noise levels

During the main behavioural experiment and in each of the 3 days of the main tRNS experiment, the observers repeated the same task and procedure. However, in this session, CM was displayed with 14 different dot densities constituting 14 noise levels. Starting from 20, the following numbers of dots were chosen on a quasilogarithmic scale: 20, 29, 41, 58, 83, 118, 168, 239, 340, 485, 691, 999,

[2]Because SR does not seems to occur when accuracy is greater than or equal to 75% (i.e., when the signal is at or above threshold; Ward et al., 2002), the SNR was maintained at a subthreshold level (70% ± 5%) in the main experiment.

1403 and 2000 (Zanker, 1995). This parameter varied randomly across trials, and the target's (sub)threshold moving signal was always constituted by the value (coherence level) measured in the threshold verification phase. Note that the stimulus used for the threshold assessment and verification was a field of 100 moving dots. Hence, the baseline performance reported the actual minimum number of dots over 100 that was needed to detect a rightward movement in approximately 70% of the cases. To keep the SNR constant across different dot densities, the target dots were increased proportionally. For example, with over 100 dots, 15% corresponds to 15 dots moving coherently. With over 999 dots, the same percentage is about 150 dots.[3] The participants completed 20 trials for each dot numerosity (noise) level, for a total of 280 trials. It is important to stress that we chose the 14 noise levels because we could not predict where the performance peak would be observed under the various conditions. We thus decided to use a large range of dot densities.

We estimated accuracy in terms of proportions of correct answers at each noise level. The task's duration was about 20 min.

2.4.5 | tRNS stimulation

In the tRNS experiment, we applied three different peak-to-peak stimulation intensities: 1 mA, 2 mA and sham with a frequency of 100–640 Hz high-frequency tRNS. The stimulation was delivered by a battery-powered stimulator (BrainStim, EMS, Bologna, Italy) through a pair of saline-soaked sponge electrodes (Figure 2) of 5 cm × 7 cm (surface 35 cm^2). In the real conditions, the current was applied for 20 min (with 10-s fade-in and -out periods at the stimulation's beginning and end). In the sham tRNS, the current was turned off 10 s after the beginning of the stimulation (with 10-s fade-in and -out periods, for a total of 30 s).

The electrodes were firmly attached to the head on the region of interest with elastic bands, and an electroconductive gel was applied under the sponges to reduce contact impedance (Fertonani et al., 2015). Only a few participants reported mild skin sensations, which disappeared after a few seconds of stimulation. The participants were asked at the end of each session by the experimenter whether they felt fatigued and whether they could feel the presence of the stimulation (Fertonani et al., 2015). No participants reported experiencing fatigue during the test, and they were not able to discriminate between real stimulation and placebo, as confirmed by a Pearson's Chi-Square test for frequency distribution ($\chi 2_{[2]} = .19$, $p = .91$; the observed probability of reported 'stimulation present' was .5 in the 1-mA tRNS condition, .54 in the 2-mA tRNS condition and .46 in the sham condition).

The electrodes were placed bilaterally about 3 cm above the inion and laterally separated from the inion by 5.5 cm. These positions should correspond to the middle temporal area in most of the participants (see also electrode positioning in previous studies that aimed to stimulate MT+; Antal et al., 2004; Zito et al., 2015; Battaglini et al., 2017, 2020).

[3]Round to the nearest decimal or integer.

3 | RESULTS

Using our data, we decided to test for the presence of an SR-like phenomenon with preplanned comparisons (paired-sample *t*-tests with Hochberg's sequentially acceptive step-up Bonferroni procedure) between peak performance (highest performance value) and the performance obtained at other noise levels. We repeated this procedure for each tRNS condition.

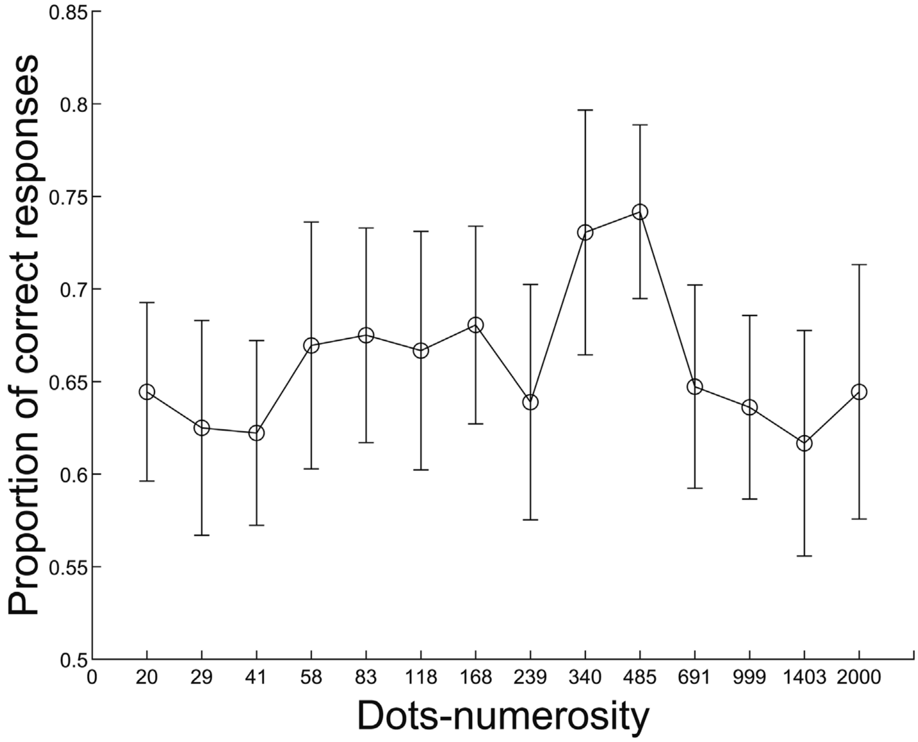
3.1 | Behavioural experiment

The individual proportion of correct answers was calculated for each of the 14 random dot numerosity levels (Figure 3). We conducted a one-way analysis of variance (ANOVA) with dots numerosity as a main within-subject factor producing significant results ($F_{[13,221]} = 2.7$; $p = .001$; $\eta^2_p = .14$). Peak performance occurred with a dot numerosity of 485. To test whether the performance obtained with 485 dots was significantly higher than the performance measured at the other levels, we computed separated paired-sample *t*-tests with Hochberg's (1988) sequentially acceptive step-up Bonferroni procedure. The *t*-tests revealed that the performance level achieved with 485 dots was significantly higher than the performance levels achieved with 20 ($p = .0024$, Cohens' $d = .68$), 29 ($p = .001$, Cohens' $d = .76$), 41 ($p < .001$, Cohens' $d = .82$), 239 ($p = .003$, Cohens' $d = .65$), 691 ($p < .001$, Cohens' $d = .63$), 999 ($p = .001$, Cohens' $d = .73$), 1403 ($p < .001$, Cohens' $d = .8$) and 2000 ($p = .007$ Cohens' $d = .59$) dots.

3.2 | tRNS experiment

We ran a two-way ANOVA with two main factors: stimulation condition (1 mA, 2 mA and sham) and dot numerosity. The main effect of dot numerosity ($F_{[7.192,165.416]} = 5.2$; $p < .001$, $\eta^2_p = .19$) was significant. The main effects of

FIGURE 3 Results of Experiment 1. Empty dots represent mean values, and error bars represent 95% confidence intervals.



stimulation condition ($F_{[2,46]} = 2.8$; $p = .069$, $\eta^2_p = .11$) and of the interaction between stimulation condition and dot numerosity ($F_{[26,598]} = 1.3$; $p = .125$, $\eta^2_p = .06$) were insignificant. Despite the absence of interaction, our initial goal was to reveal the modulatory effect of tRNS and dot numerosity on integrative mechanisms. The 1-mA tRNS and sham conditions clearly showed peak performance at different dot numerosity values (Figure 4). Indeed, the results of a two-way ANOVA performed on the latter two conditions only (i.e., with the 2-mA tRNS excluded from the analysis) showed that the main effect of the stimulation condition ($F_{[1,23]} = .14$; $p = .71$, $\eta^2_p = .006$) was insignificant, whereas the main effect of dot numerosity ($F_{[13,299]} = 3.7$; $p < .001$, $\eta^2_p = .14$) and the interaction between the stimulation condition and dot numerosity ($F_{[13,299]} = 4.4$; $p < .001$, $\eta^2_p = .16$) was significant. We also explored performance as a function of dot numerosity separately for the three stimulation conditions. For 1 mA, the effect of dot numerosity was statistically significant ($F_{[13,299]} = 4.75$; $p < .001$, $\eta^2_p = .17$). The peak in the 1-mA tRNS stimulation condition occurred at 118 dots (see Figure 4). We used paired-sample *t*-tests with Hochberg's (1988) sequentially acceptive step-up Bonferroni procedure to compare the performance at 118 dots with the performance at the other dot numerosities. Except for the comparison between 118 and 83 dots, all the *t*-tests revealed better performance with 118 dots than with the other dot numerosity values ($p_s < .01$, $.62 <$ Cohen's $d_s < 1.41$). For the sham condition, the effect of dot numerosity was statistically significant ($F_{[13,299]} = 3.3$; $p < .001$, $\eta^2_p = .13$). The peak performance occurred at 485 dots as in the behavioural experiment (see Figure 4), and according to Hochberg's (1988) procedure, it was significantly better than for all the other dot numerosity values ($p_s < .027$, $.6 <$ Cohen's $d_s < 1.24$).[4] In the 2-mA tRNS condition, there was no evident performance peak (see Figure 4); indeed, the effect of dot numerosity was not statistically significant ($F_{[13,299]} = 1.6$; $p = .1$, $\eta^2_p = .06$).

[4]Hochberg's (1988) procedure can be summarized as follows. First, we computed separate *t*-tests comparing the largest mean proportion of correct responses (corresponding to peak performance) with all the other means. Second, the tests were ordered by their *p*-values in descending order, starting with the test with the largest *p*-value. According to the procedure, if the largest *p*-value is smaller than α (with $\alpha = .05$), then all tests are significant. If the largest *p*-value is equal or larger than α, then it is non-significant and the second largest *p*-value is evaluated. If this second largest *p*-value is smaller than $\alpha/2$, then all remaining tests are significant. If not, the third-largest *p*-value is compared with $\alpha/3$, and so on. With respect to the classic Bonferroni procedure, Hochberg's (1988) procedure allows to increase the power of post hoc tests as it controls the false discovery rate, rather than type I error. When using a stricter correction such as the classical Bonferroni correction, we found that the peak performance in the 1-mA condition (118 dots) was significantly better than performance at 20, 58, 485, 999, and 1403 dots. Peak performance in the sham condition (485 dots) was significantly better than performance at 29, 58, 239, 1403, and 2000 dots. To summarize, even when applying a stricter correction, the peak performance in the sham and 1-mA conditions was significantly better than the performance at many numerosity levels.

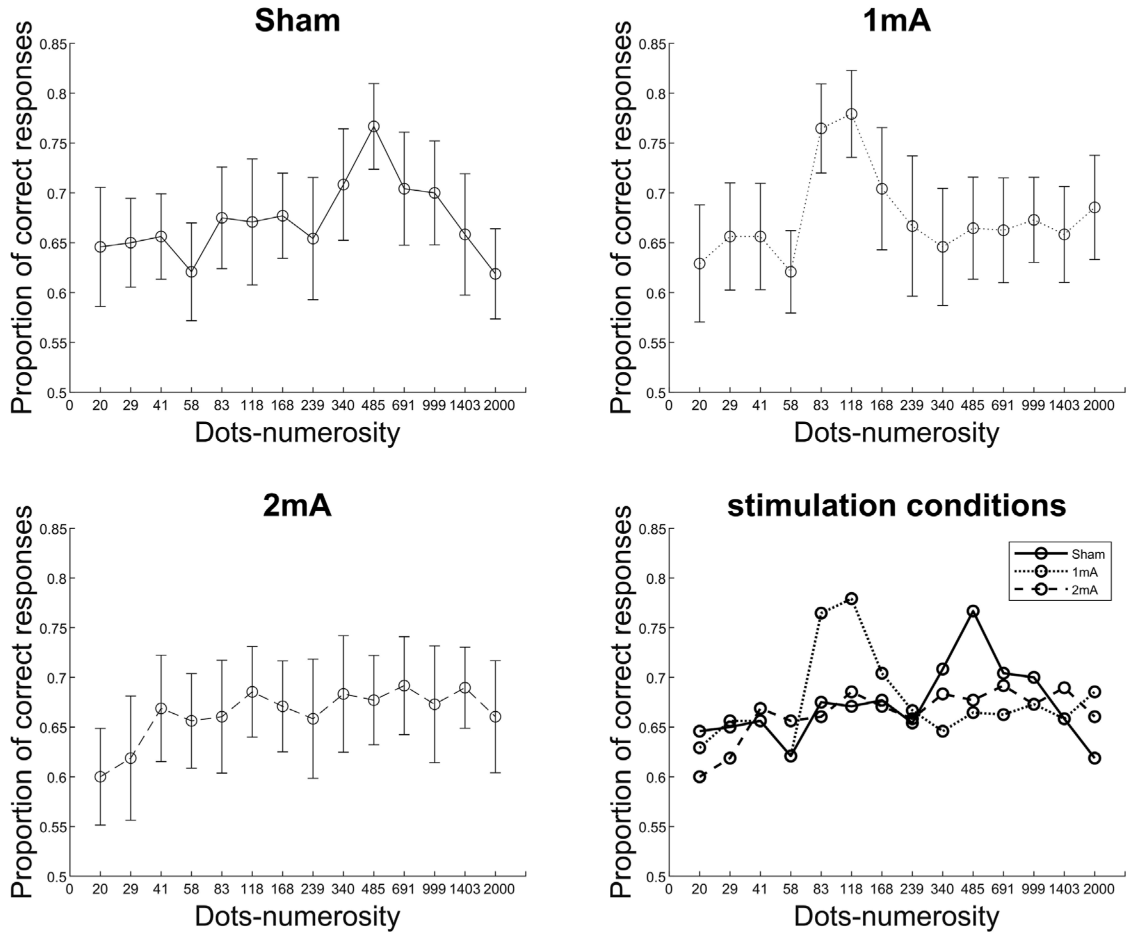


FIGURE 4 The result of Experiment 2. The upper and lower left panels represent data obtained under different stimulation conditions. Empty dots represent mean values, and error bars represent 95% confidence intervals. The peak performance in the sham condition is visible at 485 dots, whereas with 1-mA tRNS, peak performance occurred at 118 dots. In the 2-mA tRNS condition, there was no evident peak in performance. The bottom right panel illustrates clearly that in the 1-mA condition, the peak occurred with a lower dot numerosity than that achieved under the sham condition.

3.3 | EN analysis

Suppose that K is the total number of dots and that P is the number of coherent dots (i.e., dots moving in the target direction). According to the model and terminology developed by Pavan et al. (2019), in each CM discrimination trial, a number (n) of dots is sampled from the whole set of K dots, and the participants detect the CM when at least one of the sampled n dots is a CM dot (i.e., a dot that moves in the target direction). The probability of sampling a CM dot and thus providing a correct response increases with n and decreases with the K/P ratio. In this model, it is important to define two terms: local noise (i.e., precision in estimating the direction of each dot's movement) and sampling (i.e., the number of such estimates one can average; Dakin et al., 2005). According to the EN model, a given amount of local noise is added to the CM signal, and an indirect estimate of local noise is obtained through $f_{\max}$, which is the response accuracy when all the dots are CM dots (i.e., when $K/P = 1$).

By means of a series of computations based on combinatorics and an empirical estimation of $f_{\max}$ (see Table 1 and Appendix A), EN analysis allows estimation of the average number (n) of dots sampled by each participant for each level of dot numerosity (behavioural experiment; see Figure 5) and for each combination of dot numerosity and stimulation condition (tRNS experiment; see Figure 5). Please recall that n is a measure of sampling efficiency; therefore, if n is the same at two dot numerosity levels (e.g., 85 and 400 dots), for those two dot numerosity levels, the sampling efficiencies are equal.

Regarding the origins of the SR-like phenomenon observed in the behavioural and tRNS experiments, if the pattern observed in the behavioural and tRNS experiments reflects variations in sampling efficiency, a similar result pattern should emerge for the estimated number

TABLE 1 f_{max} obtained for the 14 levels of noise.

Dot numerosity	20	29	41	58	83	118	168	239	340	485	691	999	1403	2000
Mean	.99	.98	.98	.99	.99	.99	.97	.99	.97	.99	.96	.97	.97	.97

Note: The f_{max} parameter was estimated on a sample of 10 different participants.

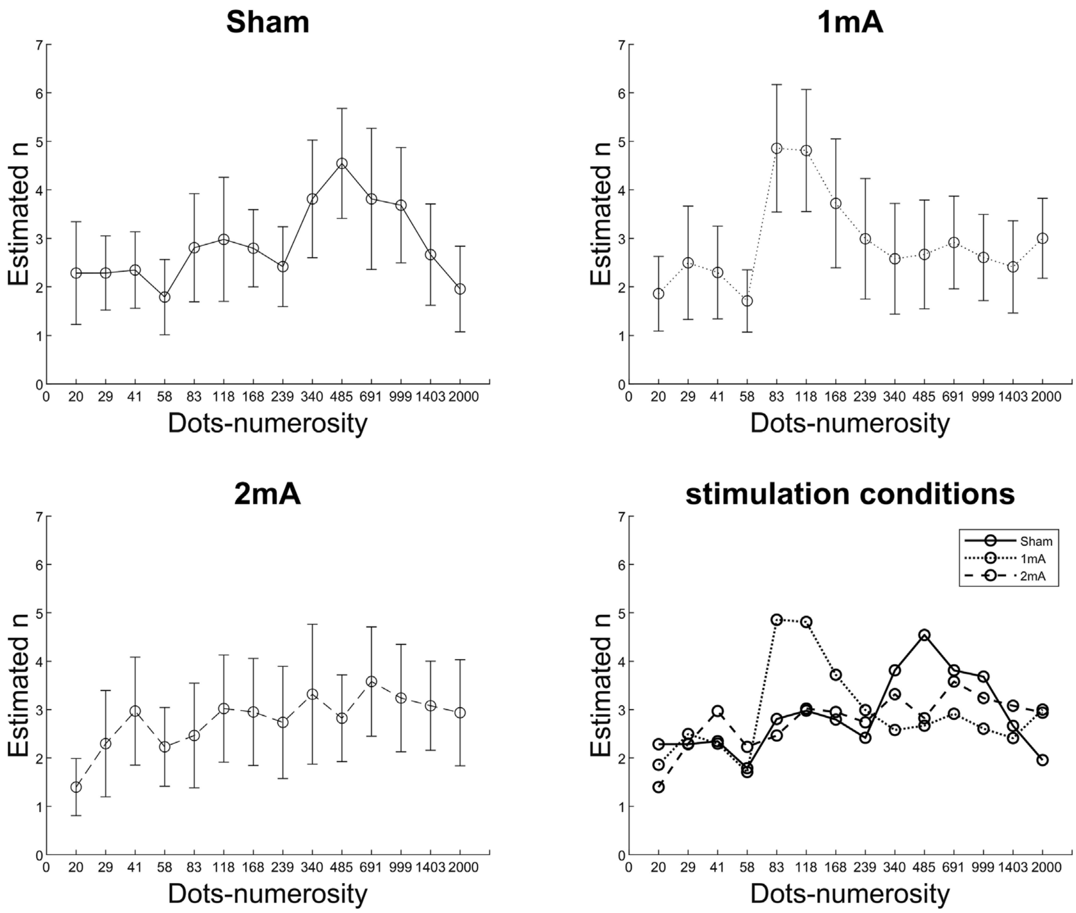


FIGURE 5 The top and bottom left panels represent estimated n obtained in different stimulation conditions (sham, 1 mA, 2 mA). Empty dots represent the mean values, and error bars represent 95% confidence intervals.

(n) of dots sampled by the visual system for each level of K. The analyses depicted in Figure 5 support the hypothesis that external noise and neural noise affect CM discrimination through a modulation of sampling efficiency.

4 | DISCUSSION

The present study investigated the mechanism that may improve global motion integration in a CM detection task. First, we aimed to explore whether an improvement of motion signal integration could emerge when variations in external noise were obtained by varying the total number of dots while keeping the SNR constant. Second, we explored whether the neural noise modulation, obtained by applying tRNS to the visual cortex during CM detection task, interacts with external noise to modulate behavioural performance.

At all levels of the experiment, stimuli (i.e., external noise) were presented with a baseline SNR fixed at sub-threshold levels. We found that the participants' accuracy in detecting CM, as a function of the number of dots, showed a clear peak at dot numerosity levels specific to the two conditions (i.e., with and without tRNS). The peak shifted towards lower dot numerosity levels when 1-mA tRNS was applied compared to the sham and the behavioural conditions. No peaks were observed at 2 mA.

Figure 3, which represents Experiment 1's results, showed a peak in performance at 485 dots in the visual stimulus. This is in agreement with our hypothesis. Indeed, we suggested that by increasing the number of dots while leaving the SNR fixed, more detectors are recruited, which can enhance integrative mechanisms, but when there are too many random dots, the external noise ends up masking the coherent dot movement. In other words, this result indicates the existence of an SR-like phenomenon. Previous papers have reported that the number of dots displayed in a stimulus (dot density) has only a modest effect on global CM tasks (Barlow & Tripathy, 1997, Scase et al., 1996, Watamaniuk, 1993, Williams & Sekuler, 1984), but none of these studies tested performance at very high dot numerosity levels. To the best of our knowledge, the experiments presented in this manuscript represent the first attempt to reveal the effects of large dot numerosity on global CM tasks. The results of Experiment 2 showed that the 1-mA tRNS caused a clear shift in the peak performance. This is not the first evidence that electrical stimulation can affect global CM motion perception. For example, direct current stimulation can improve motion discrimination (Battaglini et al., 2017) and motion detection (Battaglini et al., 2020) at threshold levels. The novelty of our result is that, on the one hand, 1-mA tRNS can induce a peak in behavioural performance at a smaller dot numerosity than in the sham condition, suggesting that random noise electrical stimulation can enhance integrative mechanisms. On the other hand, increasing the strength of the tRNS (to 2 mA) seems to disrupt integrative mechanisms. We speculate that 2-mA tRNS might introduce excessive noise to the perceptual system, negatively affecting global motion direction discrimination. This idea was also suggested by Pavan et al. (2019) because their results revealed a deleterious effect of 2.25-mA tRNS on global motion processing.

Taken together, these results are consistent with our initial hypothesis and expand on the results obtained by van der Groen and Wenderoth, 2016 and Pavan et al. (2019). Indeed, we showed that is possible to use both neural and external noise to produce and modulate an SR-like phenomenon in a CM detection task.

Our findings could have some clinical application. To summarize, modulating the quantity of external noise in the perceptual stimulus or modulating the strength of tRNS can increase the likelihood of detecting a target at a subthreshold level, probably producing an SR-like phenomenon. This could be used to boost visual perceptual learning (i.e., the ability to improve perception skills through a repetitive task [training] with stimuli presented at a weak intensity). Perceptual learning has often been implemented to improve vision in clinical populations (Barollo et al., 2017; Casco et al., 2018; Maniglia et al., 2016), but it requires many sessions (even months) to produce results. Increasing the likelihood of detecting a weak-intensity stimulus in every single trial might reduce the number of training sessions that are needed to achieve improvement. However, to take true advantage of SR-like phenomena, it is important to consider all sources of noise. For instance, in our CM task, 1-mA tRNS could have been an optimal stimulation level for our young participants, but what about other populations? A neurocomputational SR model reveals that elderly individuals need more noise to elicit SR (Li et al., 2006), so 1-mA tRNS might not be appropriate for this population. People with autism spectrum disorder have problems with filtering out external noise (Park et al., 2017); therefore, we expect that a lower number of dots might be needed to reach a peak in performance among this population compared with among other participants.

In the behavioural and sham conditions, we observed that a peak occurred when many dots (485 dots) were displayed. Thus, we wondered why the CM peak occurred when participants viewed a relatively high number of dots. Through an EN analysis, we estimated the average number (n) of dots sampled by each participant for each level of dot numerosity and for each dot numerosity–stimulation condition combination. The results of this analysis allow us to speculate about how integrative mechanisms of CM are modulated in the experimental conditions tested in this study. The results suggest that the highest possible sampling efficiency occurs at a relatively high number of dots, when the number of detectors responding to the moving dots is thus relatively high. More formally, n—that is, a measure of efficiency of motion signal integration—revealed that the maximum sampling efficiency of coherent dots was reached at the peak of the performance, both with and without tRNS applied (see Figure 4): at approximately 80 dots in the tRNS condition and at approximately 400 dots in the sham condition. As predicted, when neural noise was added through tRNS, a smaller number of dots (i.e., external noise) was necessary to achieve the maximum sampling efficiency than was required when no tRNS-induced noise was present. This supports the conclusion that external and neural noise affect motion discrimination through a common mechanism of motion signal integration.

Here, we push forward the hypothesis of a sampling efficiency mechanism to explain the SR-like phenomenon. On the contrary, it is unlikely that the reduction of local noise may also be a factor (local noise impairs the accuracy of the observer's depiction of each element's motion). Indeed, Dakin et al. (2005) demonstrated that local noise decreases with the number of dots, but this effect saturates at a relatively low number of dots, approximately 60 dots, that is, below the range of numerosity levels within which the SR peak fluctuates both with and without tRNS. Conversely, integrative capacity improves at a larger range of numerosity levels (from 60 to 256 dots). Moreover, our EN analysis showed that $f_{\max}$ was close to 1 at each dot numerosity level (Table 1), which is inconsistent with the alternative interpretation that the SR-like phenomenon reflects a reduction of local noise.

Based on these observations, we are inclined to suggest that the effect of tRNS is that it increases sampling efficiency—that is, the integrative capacity underlying CM (Dakin et al., 2005; Pavan et al., 2019). These considerations bring us to two additional questions: What does the improvement of sampling efficiency induced by applying tRNS comprise? Is there a specific integrative mechanism that is more suitable to be improved by tRNS? Webb et al. (2007) and Dakin et al. (2005) evaluated the relative efficiency of different CM algorithms: population averaging, winner-take-all and the maximum likelihood mechanism. Population averaging is an unlikely candidate because its response depends on the SNR only. Moreover, any stimulus-based statistical estimate of central tendency fails to account for psychophysical data. Maximum likelihood estimation could account for numerosity and tRNS effects because it relies on a likelihood function that represents the probability that a range of motion directions gives rise to a specific the neural response. The winner-take-all method relies on the most active directionally tuned columns of preferred directions (the preferred direction of the most active mechanism). According to Webb et al. (2007), 'mechanism-based, read-out algorithms offer an accurate and robust guide to human motion perception'; however, the maximum likelihood method seems superior because the variance of this algorithm is consistently smaller than that of the winner-takes-all algorithm. An interesting question is whether the tRNS action is more consistent with one or the other of these two mechanisms. Although the physiological mechanism of tRNS action should be further explored, it has been shown that tRNS adds noise in the brain by acting on the dynamics of sodium channels (Potok, Bächinger, et al., 2021a; Remedios et al., 2019), possibly causing a weak depolarization of the cell membrane (Schoen & Fromherz, 2008) and increasing cortical excitability (Potok, Bächinger, et al., 2021a; Potok, van der Groen, et al., 2021b). Therefore, neural noise added by tRNS might facilitate the processing of near-threshold signals, thus improving signal detectability (see, e.g., Fertonani et al., 2011). In short, neural noise added by tRNS increases the response of the neurons in the pool regardless of whether they are sensitive to target motion. This conclusion does not conflict with a maximum likelihood algorithm (Webb et al., 2007). However, the tRNS facilitation is likely to be more conspicuous for the neurons with direction tuning close to that of the target because their state-dependent nature of noise is near the physiological threshold. Consequently, these neurons likely have a major role in determining the final response, and the larger their number (i.e., n of neurons close to threshold), the higher the probability of CM response. The tRNS effect could therefore be interpretable because it would make the integrative mechanism more likely to use a winner-take-all computation.

So far, we have discussed mechanisms that probably act on the early and middle stages of motion computation. Recently, another interesting study suggested that tRNS can induce an SR-like phenomenon (van der Groen et al., 2018) in a global CM task. The authors used a drift diffusion model to measure the influence of different component processes involved in simple decision-making tasks. The model indicated that tRNS increased the rate of evidence accumulation—that is, a measure of how rapidly evidence is accumulated (which depends on the quality of evidence in the stimulus). However, the benefit of tRNS appeared only when stimuli were just below the threshold and not when they were well above or well below the threshold. Therefore, the authors concluded that tRNS can cause an SR-like phenomenon that affects perceptual decision making (i.e., a late stage of motion computation). The drift diffusion model requires reaction times that we did not measure in the present study. In future research, it would be interesting to directly compare early (decoding and encoding) and late (perceptual decision making) motion perception mechanisms.

Finally, some limitations of the present study should be taken into account. One is the lack of an a priori sample size analysis, as we simply chose a sample size similar to those used in previous studies on this topic, and the arbitrary range of numbers of dots chosen. Moreover, in the current study, we assessed the baseline performance only at the beginning of the first session of the tRNS experiment (threshold assessment and verification), despite the fact that the threshold on a perceptual motion task might significantly improve with practice. However, a massive amount of practice appears to be necessary for threshold improvement in this context. Matthews and Welch (1997) showed a modest amount of learning using CM discrimination task with participants that completed about 5000 trials. In our design, the total number of trials was 840, which is probably insufficient to produce a significant effect of practice or of perceptual learning. To support this speculation, we ran an additional ANOVA with Day (Day 1, 2 and 3) and the 14 random dot numerosity levels as within-subject factors. The effect of Day ($F_{[2,46]} = 1$; $p = .38$, $\eta^2_p = .04$) or the interaction Day × Dots numerosity ($F_{[26,598]} = .8$; $p = .67$, $\eta^2_p = .04$) was not significant.

Another limitation is that our experiments do not afford a direct exploration of the relationship between tRNS induced, cortical excitability and behavioural changes, because we did not record electrophysiological signals. A previous study revealed that 20 min of high-frequency tRNS (as in our study) applied over the occipital cortex significantly changes cortical excitability up to 60 min post-stimulation, lowering phosphene thresholds evaluated by TMS (Herpich et al., 2018). Therefore, according to the results of Herpich et al. (2018), high-frequency tRNS might have modulated cortical excitability, leading to a gradual improvement of participants' performance. To provide an exploratory test of the possible presence of this effect, we applied generalized mixed-effects logit models (Jaeger, 2008) on the response accuracy in the 1-mA stimulation condition, where the tRNS effect was present, with the number of trials as fixed effect and the by-subject intercept as the random effect (R package lme4; Bates et al., 2015). Accuracy did not vary with the number of trials, neither when all dots numerosities were considered ($b \approx 0$, $p = .72$), nor when only the specific dots numerosities associated with a peak in the performance were considered (i.e., $n = 83$ and $n = 118$; $b = -.001$, $p = .27$). The data do not allow us to speculate any further on this issue.

5 | CONCLUSION

In conclusion, we showed that external and neural (tRNS-induced) noise are involved in producing an SR-like phenomenon. We determined that noise can be important in coding the optimal strategy through integrative operation of a neural pool, confirming the need to frame brain stimulation effects using a network activity-dependent model (Fertonani & Miniussi, 2017).

AUTHOR CONTRIBUTIONS

Luca Battaglini: Conceptualization; formal analysis; methodology; software; writing–original draft; writing–review and editing. **Clara Casco:** Conceptualization; funding acquisition; methodology; writing–original draft; writing–review and editing. **Anna Fertonani:** Conceptualization; data curation; writing–original draft. **Carlo Miniussi:** Conceptualization; writing–original draft; writing–review and editing. **Michele Di Ponzio:** Data curation; writing–original draft; writing–review and editing. **Michele Vicovaro:** Formal analysis; methodology; writing–original draft; writing–review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The datasets analyzed during the current study are available in the OSF repository.

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APPENDIX A

The model developed by Pavan et al. (2019) relies on the assumption that a correct response is provided when, among the n dots randomly sampled by the visual system, at least one dot is a CM dot. Predicted response accuracy f is defined by Equation (1):

$$f = \frac{1}{2} + \left(f_{\max} + \frac{1}{2}\right) g \tag{1}$$

where $f_{\max}$ is response accuracy when all the dots are CM dots and g is the probability that at least one CM dot is present in an n-tuple of randomly sampled dots. Please recall that $f_{\max}$ is conceived as an indirect measure of local noise that interferes with CM motion detection (i.e., $f_{\max}$ decreases when the level of local noise is high).

The probability g can be obtained through combinatorics. For a given set of parameters K, P and n, the probability g corresponds to one minus the probability that, in an n-tuple of randomly sampled dots, none of the dots is a CM dot. The latter corresponds to the ratio between $\binom{K-P}{n}$, which is the total number of n-tuples that do not contain any CM dot, and $\binom{K}{n}$, which is the total number of n-tuples. The probability g is thus defined by Equation (2):

$$g = 1 - \frac{(K-P)!(K-n)!}{K!(K-P-n)!} \tag{2}$$

Because in the behavioural and the tRNS experiment the signal-to-noise ratio was kept constant for each participant, in Equation (2), it is convenient to replace P with $K \times SNR$, where SNR is the signal-to-noise ratio (i.e., P/K). Using the Gamma function to extend the factorial function to complex numbers $(x! = \Gamma(x+1])$ and substituting g in Equation (1), Equation (3) is obtained:

$$f = \frac{1}{2} + \left(f_{\max} + \frac{1}{2}\right)\left(1 - \frac{\Gamma(K - K \times SNR + 1)\Gamma(K - n + 1)}{\Gamma(K+1)\Gamma(K - K \times SNR - n + 1)}\right) \tag{3}$$

Now, K is a manipulated variable, SNR is an empirically determined value that remained constant for each participant in the two experiments and f is response accuracy. In order to estimate $f_{\max}$, a supplementary experiment was conducted. The apparatus, method and procedure were the same as in the main experiment (CM detection task with 14 levels of noise), except for the fact that the SNR was kept fixed to 1 for all the participants. Ten observers participated in this experiment. The sample size was smaller than the behavioural and tRNS experiments, because of the reduced variability among participants that resulted in a smaller standard error on the associated $f_{\max}$ parameter. Please note that in the following computations, we use the empirically estimated $f_{\max}$ values both for the behavioural and for the tRNS experiment (all stimulation conditions). Indeed, the results reported by Pavan et al. (2019) suggest that $f_{\max}$ is not affected by stimulation.

Because the values of K, SNR, f and $f_{\max}$ are known, we could estimate n for each participant and each experimental condition. Specifically, Equation (3) (with Ramanujan's factorial approximation) was used to calculate f for each value of n in the range [0.01 10], step 0.01. For each participant and each experimental condition, we selected the value of n that minimized the absolute difference between the calculated and the experimentally observed f. The results are reported in the main text.