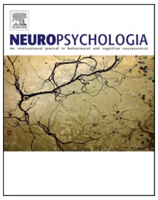
Neuropsychologia 168 (2022) 108174

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia



Stochastic resonance at early visual cortex during figure orientation discrimination using transcranial magnetic stimulation

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ARTICLE INFO

Keywords:
Stochastic resonance (SR)
Early visual cortex
Figure discrimination
Initial stage
SR characteristics
Transcranial magnetic stimulation (TMS)

ABSTRACT

Visual noise usually reduces the visibility of stimuli. However, very low contrast or subliminal visual noise can sometimes enhance the visibility of low-contrast stimuli. It has been suggested that this enhancement occurs at the visual cortex. The aims of this study are to clarify the role of the early visual cortex (V1/V2) in the enhancement effect and to clarify the relationship of the SR characteristics among different experiments. Noise was added directly to the visual cortex by using transcranial magnetic stimulation (TMS) with randomly varying intensity. The location on the scalp and the timing (stimulus onset asynchrony, SOA) of TMS were specifically adjusted to target the early visual cortex. Contrast thresholds for figure orientation discrimination were measured as a function of TMS noise intensity. With increasing TMS noise intensity the contrast threshold for figure discrimination first decreased (enhancement) and then increased (impairment). These effects were clearly dependent both on scalp location and timing (SOA). The optimum SOA was around 60 ms, while the optimum location varied across participants. Outside the optimum location and SOA values, no TMS effects were found. The enhancement effect can be accounted for by the stochastic resonance (SR) theory based on a threshold device. In addition, we reveal similarity in characteristics of the SR phenomenon between different experiments.

1. Introduction

There has been a lot of interest in research that attempts to answer the question of whether the human brain can produce stochastic resonance phenomena (SR phenomena). SR is a nonlinear phenomenon whereby the addition of a random noise can enhance the detection of weak stimuli or enhance the information content of a signal. An optimal small amount of added noise results in the maximum enhancement, whereas further increase in the noise intensity reduces information content and degrades perception. This enhancement phenomenon is contrary to our intuition, and research has been conducted to confirm whether this phenomenon really exists. As a result, the existence of this phenomenon is widely known in nature (Benzi et al., 1981; Douglass et al., 1993; Wiesenfeld and Moss, 1995; Collins et al., 1997; Gammaitoni et al., 1998; Yamazaki et al., 1998; Moss et al., 2004).

SR phenomena in the human brain have been demonstrated experimentally (Simonotto et al., 1997; Collins et al., 1997; Zeng et al., 2000; Kitajo et al., 2003, 2007; Ward et al., 2010; Abrahamyan et al., 2011, 2015; Schwarzkopf et al., 2011; Van der Groen and Wenderoth, 2016). A detailed review on sensory information processing was reported by Moss et al. (2004). Collins et al. and Zeng et al. reported the SR phenomenon in human tactile sensation and in human hearing ability, respectively. Simonotto et al. (1997) analyzed the SR phenomenon using SR theory based on a threshold device model, which was very simple model of neural activity. Results showed that the detection performance to adding noise intensity was consistent with that theory. Kitajo et al. (2003, 2007) and Ward et al. (2010) reported SR mediated synchronization of neural activity. Apart from those, there were studies applied transcranial magnetic stimulation (TMS) or electric current directly to the cortex in which stimulus processing was ongoing (Abrahamyan et al., 2011, 2015; Schwarzkopf et al., 2011; Van der Groen and Wenderoth, 2016). These studies showed that enhancement in the performance was caused by direct stimulation of the brain. Schwarzkopf et al. (2011) delivered TMS to the motion sensitive complex V5/MT by locating the TMS device accordingly on the scalp. They applied triple-plus TMS (pulse gap of 50 ms) immediately after motion stimulus. Abrahamyan et al. (2011, 2015) used single-pulse TMS, it's delay time from onset of visual stimulation, stimulus onset asynchrony (SOA), was around 100 ms, which indicates

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https://doi.org/10.1016/j.neuropsychologia.2022.108174
Received 2 November 2021; Received in revised form 25 January 2022; Accepted 6 February 2022
Available online 8 February 2022

that stimulating area was at a higher level than V1/V2, but it was unclear at which sub-area of the visual cortex did the SR phenomenon occurred. Van der Groen and Wenderoth (2016) targeted the overall visual cortex with their transcranial random noise stimulation (tRNS), without specifying any sub-area of the visual cortex. Further, the tRNS was presented during the whole duration of stimulus presentation, which was 2.02 s. Therefore, their studies did not allow an accurate localization of the SR effect in space or time.

The brain, by the way, has a functional localization. The signal from a sensory organ inputs into the corresponding cortical areas, and the final recognition is done through the paths of sub-areas. That is, recognition is undergone through different sub-areas both spatially and temporally. To understand the relationship between SR phenomena and cognitive functions in the brain, it is necessary to take these processes into account. In the present work, we clarified the role of the early visual cortex in the SR phenomenon during figure orientation discrimination and the relationship of the SR characteristics among different experiments. TMS targeted the early visual cortex, especially V1 (or possibly V2). This was achieved by choosing appropriate ranges of SOA (stimulus onset asynchrony) and location on the scalp based on earlier literature. The SR characteristics among ours, single neurons and contrast detection of human vision were discussed through the SR theory based on a threshold device model. These will be described in detail later in this paper.

2. Materials and methods

2.1. Participants

Ten healthy male students (22–23 years old) who were naïve to the purpose of the study were included. They were divided into two groups. One group ($n = 5$) participated in the experiment involving TMS (TMS-experiment) and the other group ($n = 5$) participated in the visual figure discrimination experiment alone (click-sound-experiment). Purpose of the latter group was to examine the effects of the click-sound from TMS coil. The participants were not paid for participating. Their averaged age was 22 years, and all of them had normal or corrected-to-normal vision. The details of the experiment were explained to them, and informed consent was obtained. The study design was approved by the ethics committees of Fukuoka Institute of Technology, Japan and Helsinki University Hospital, Finland.

2.2. Visual stimulus

The visual stimulus was a U-shaped figure subtending a square of $0.45^\circ \times 0.45^\circ$ with an opening of $0.15^\circ \times 0.3^\circ$ pointing to the left or right. The presentation duration of the U-shaped figure was 20 ms; its location on a 17- inch CRT display (SONY CPD E220) was at the lower left quadrant at an angular distance of 1.0° from a fixation point. The fixation point of $0.06^\circ \times 0.06^\circ$ was presented at the center of the CRT display. The refresh rate of the CRT was 100 Hz, the resolution was 1024×768 and the background luminance was 22 cd/m^2. The Weber contrast was calculated as $(L_t - L_b)/L_b$ with $L_t =$ luminance of the visual stimulus and $L_b =$ luminance of the background screen. Luminance levels were measured with a photometer (Minolta CS1000). We prepared twelve visual stimuli with six different contrast levels and two different orientations (left and right) for each participant.

2.3. Transcranial magnetic stimulation

TMS was produced by a monophasic magnetic stimulator (Magstim 200) with a 70 mm figure-of-eight coil. TMS intensity was described as a percentage of the maximum output magnetic field of the stimulator. There was a time delay between the onset of the presentation of a visual stimulus and the start of TMS stimulation (stimulus onset asynchrony; SOA). TMS intensity was determined on the basis of the percentage of the maximum output magnetic field of the stimulator, and it was varied in different experiments. Experiments were performed under various SOAs (35–105 ms) and output TMS intensities (10–70%). These values varied across participants. All parameters related to TMS-experiment are listed in Table 1.

The vertical coil location was set 2 cm above the inion as described in previous studies (Becker and Zeki, 1995; Silvanto et al., 2005), and lateral position was set in a range of 0.0–2.0 cm to the right of the inion because the visual stimulus was presented to the left visual field. The coil was positioned tangentially to the skull with the handle pointing upwards and then fixed using a tripod. To prevent the declination of the coil location, the participants wore a swimming cap on which there was a grid pattern.

2.4. Procedure of stimulation

We adopted a two-alternative forced-choice method in our experimental setups. Each participant was tasked with indicating the orientation of the U-shaped figure by pressing the leftwards or rightwards pointing arrow key on a keyboard. We conducted two experiments; the first one was a TMS-experiment and the second one was a click-sound-experiment (see below). The TMS-experiment was conducted by using the constant stimuli method. The click-sound-experiment was conducted by using adaptive staircase procedure with a 2:1 rule (down after two correct answers and up after one mistake) and a step size of about 0.67 cd/m^2. The 2:1 rule corresponds to the probability of correct response of 70.7% (Wetherill and Levitt, 1965). The distance between the participant and the CRT was 57 cm. The fixation point was presented for 500 ms, and then, the U-shaped figure was presented for 20 ms. TMS was delivered with various SOAs from the start of the visual stimulus. A dark screen terminated each trial. The inter-trial interval was 5 s (see Fig. 1). One of 12 different stimuli was randomly selected in one trial, and one hundred and forty-four trials were randomly presented in one experiment. A screen with the same luminance as the background was presented for 10 s every 24 trials.

In the main experiment, contrast thresholds for the discrimination of the orientation of the U-shaped pattern were measured as a function of TMS intensity. Various SOAs (timing) and locations of the TMS stimulation were used to search for the approximately optimum values that produce an enhancement effect. These variables were varied using a heuristic, i.e., a kind of trial and error based, procedure instead of a systematic evaluation, since the two-dimensional (SOA x location) parameter space is quite large. Another reason for using this light weight heuristic procedure was that we tried to avoid the load of numerous measurements with strong magnetic stimuli on the participants. The zero (0%) intensity served as a control condition to which the results with the other intensities were compared. The search for the optimum locations for each participant is important because there are large anatomical differences in V1 and V2 cortical areas among individuals

Table 1
Coil positions and SOAs in the experiments.

Participant	Coil position (cm) (to the right from the inion)	SOA (ms)
P1	0	45, **65**, 85, 105
	1.5	65, 85
P2	1.5	45, **65**, 85
	2.0	45, 65, 85
P3	1.5	45, **55**, 65, 75
	2.0	45, 55
P4	0	45, 65, 85, 105
	1.5	35, **45**, 65, 85
P5	0	45, 65, 85, 105
	1.5	45, **65**, 85

The bolded numbers indicate the individual SOA values associated with an observed enhancement.

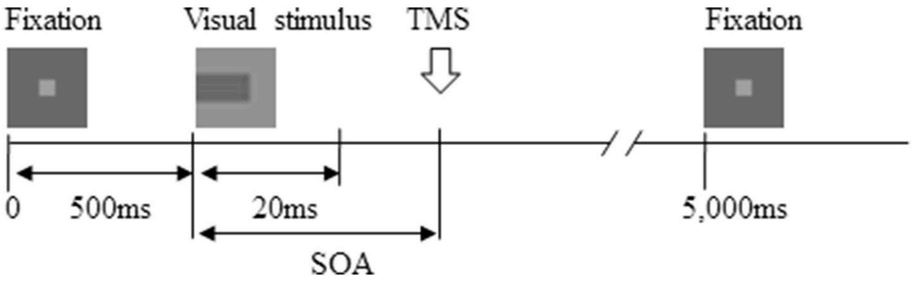

Fig. 1. Experiment design. Twenty-four trials were performed for each of 6 different contrast levels in a single experiment. The number of trials was 144 in one experiment. The contrast values and the orientation of the figure were random. The TMS intensity and SOA were fixed in a single experiment.

(Amunts et al., 2000; Bridge et al., 2005).

To confirm that the observed SR was not a non-specific effect of TMS, we performed the click-sound-experiment using a pseudo click sound generated by a computer. In the click-sound-experiment, SOA was set 65 ms which is almost the same as the mean value of SOAs when each participant showed the SR phenomenon. The computer-generated click sound mimicked the sound emitted by the TMS coil.

2.5. Data analysis

The contrast threshold was defined as a contrast at which the proportion of correct responses was 75%. This value was obtained by applying a sigmoid-logistic curve (using MATLAB). Dunnett's test (Dunnett, 1995), a multiple comparison procedure, was used to test the statistical significance of the differences between thresholds under the control condition and TMS conditions. This test is applied to compare treatments with a control, and is specifically designed to avoid Type I error (Dunnett, 1995). P-values were calculated by using the R programming language. In click-sound-experiment, on the other hand, *t*-test was used to test the statistical significance of the differences of contrast thresholds between with and without click-sound.

3. Results

3.1. Enhancement and suppression as a function of TMS intensity

The results of the main experiment are depicted in Fig. 2, which shows the percentage of change in threshold contrast as a function of TMS intensity relative to zero TMS intensity, i.e. the enhancement effect. The left side panels of Fig. 2 show the result for non-optimal TMS locations or non-optimal SOA values. In this case, TMS does not produce any statistically significant changes. Instead, on the right side panels with approximately optimal TMS location and optimal SOA show there are statistically significant changes so that with increasing TMS intensity the enhancement first increases and then decreases. Importantly, the optimum coil position is different for different participants. This result is in agreement with what could be expected, since there are large anatomical differences in V1 and V2 cortical areas among individuals as reported by Amunts et al. (2000) and Bridge et al. (2005).

Table 2 shows the results of Dunnett's multiple comparison test. Significant differences in enhancement were observed for all participants between the control and TMS conditions. The enhancement was not induced when each SOA, coil location, and TMS intensity were different from those indicated in Table 2 for each participant. Large suppression of discrimination was not observed in participant P5 at high TMS intensity. It seems that the decrease in perception might also have been observed in participant P5 if the intensity of TMS would have been strong enough as shown in the case of participant P4 (Fig. 2h). Our experiments showed that, for most participants, performance in figure orientation discrimination reached the maximum and then decreased with an increase in noise intensity.

3.2. Click-sound-experiment

We evaluated the effects the click-sound from TMS coil to figure out potential discrimination by means of the click-sound experiment. No statistical significance of the differences of the discrimination threshold were obtained between experiments with and without the click-sound. A mean *p* value of each participant obtained by *t*-test was 0.383 and a standard deviation was 0.0444.

3.3. Phosphene threshold

We measured the phosphene threshold at the coil locations where the SR phenomenon occurred. The thresholds ranged from 60 to 90% intensity, with a mean value of 73.0% and a variance of 6.7. No systematic relationship between these thresholds and TMS intensities showing the highest performance was found, in the range of our experiments.

3.4. Comparison with an SR theory

To further analyze the SR characteristics we used the very simple threshold device theory which describes the SR phenomenon of an asymmetric level-crossing detector (Jung, 1994; Gingl et al., 1995). The neural mechanisms of contrast detection in the visual cortex are complex, however. We deal only with the relationship to the SR theory as a simple example, since the purpose of this paper is not to elucidate the complex details of neural mechanisms. It is interesting to know how well the observed phenomena can be explained by a model that is highly simplified with an abstract representation of the workings of a system. We believe that it is useful as a means to investigate the common features that exist between different neural functions or neural levels.

There are several physical models based on SR theory, but a general formula for obtaining signal-to-noise ratio (SNR) is the following (Wiesenfeld and Moss, 1995; Gammaitoni et al., 1998).

$$SNR\alpha\left(\frac{\varepsilon\Delta U}{D}\right)^{2}\exp(-\Delta U/D) \tag{1}$$

Where ε is the input signal amplitude, D is the input noise intensity and ΔU is a constant related to the threshold or the barrier height. Since we are dealing with the SR phenomenon in the brain, which is closely related to neural functions, we selected the SR theory based on the threshold device model, although it is very simplified model of a neuron. The threshold device model can be described in the following way. Consider a periodic signal with an amplitude lower than the threshold value of a device, and noise is added. If there is no noise or very small noise, the signal never crosses the threshold, so the output amplitude remains zero. Here, we increase the amplitude of the noise. When the amplitude of signal plus noise crosses the threshold, a single impulse with constant amplitude is generated, similar to an action potential of a neuron. In this situation, a periodicity of the output impulse train would be similar to the periodicity of the input signal as long as the amplitude of noise is moderate. The amplitude of noise increases more, it exceeds

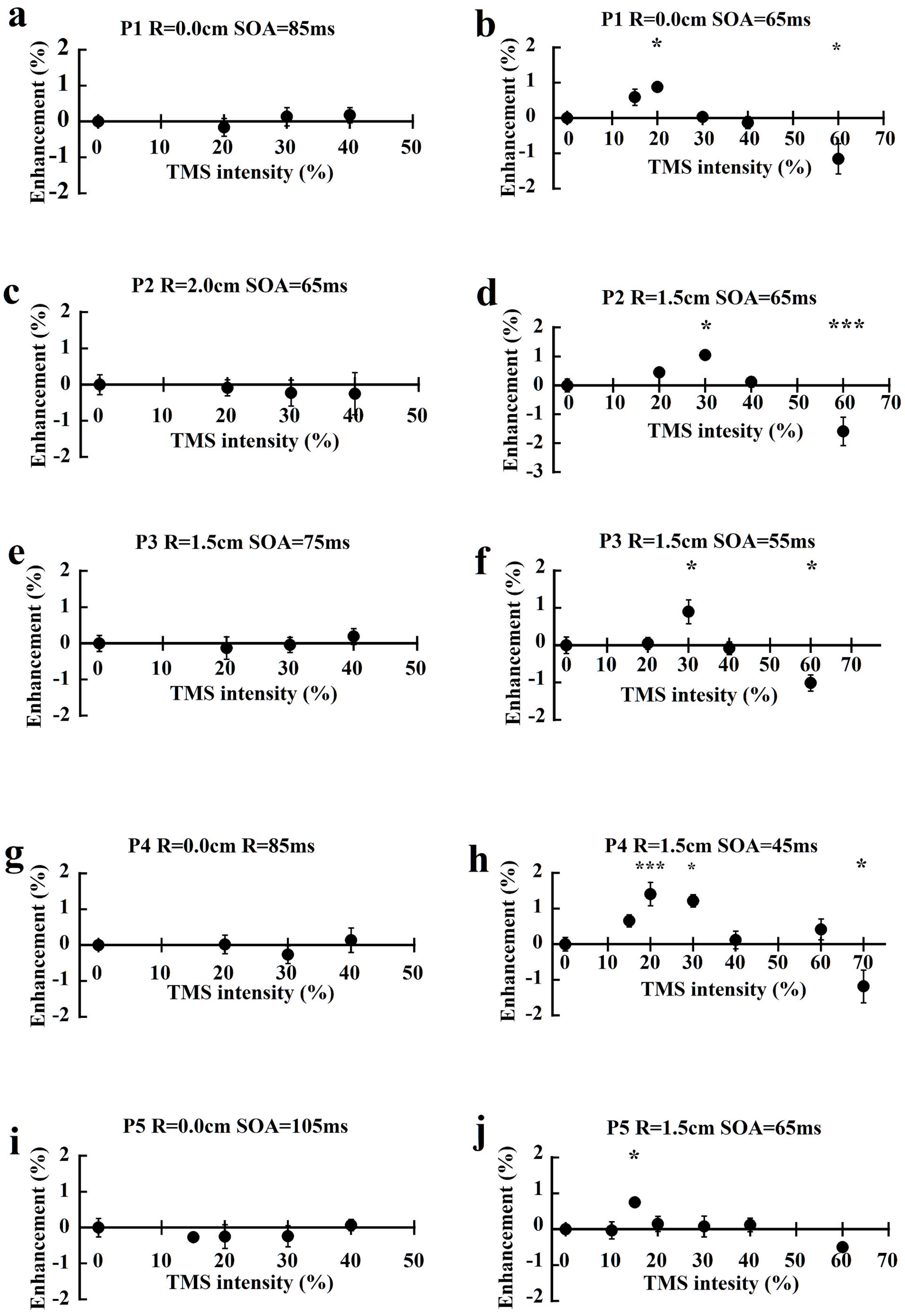

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Fig. 2. Enhancement as a function of TMS intensity. Coil positions and SOAs are as follows: participant P1: (a) coil position, 0.0 cm to the right of the inion; SOA = 85 ms; (b) coil position = 0.0 cm; SOA = 65 ms; participant P2: (c) coil position, 2.0 cm to the right; SOA = 65 ms; (d) coil position, 1.5 cm to the right; SOA = 65 ms; participant P3: (e) coil position, 1.5 cm to the right; SOA = 75 ms; (f) coil position = 1.5 cm to the right; SOA = 55 ms; participant P4: (g) coil position, 0.0 cm to the right; SOA = 85 ms; (h) coil position, 1.5 cm to the right, SOA = 45 ms; and participant P5: (i) coil position, 0.0 cm to the right, SOA = 105 ms; (j) coil position, 1.5 cm to the right, SOA = 65 ms. The vertical coil location was always 2 cm above the inion for all participants. The error bar represents ± SE. Enhancement is clearly seen in participants (the right side of Fig. 2). TMS intensity is a percentage of the full output magnetic field of the stimulator. The number of the experiments was 8 for the control condition and 6 for TMS condition. Asterisks *, **, and *** indicate $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. Items at the top of each plot describe participant, coil distance from the inion to the right side and SOA, respectively.

Table 2
Multiple comparison judgement.

Participant (ms)	SOA (lateral)	Coil location	TMS intensity (enhancement)	p-value (enhancement)	TMS intensity (suppression)	p-value (suppression)
P1	65	0 cm right	20%	0.02849	60%	0.00299
P2	65	1.5 cm right	30%	0.0219	60%	<0.001
P3	55	1.5 cm right	30%	0.0270	60%	0.0119
P4	45	1.5 cm right	20%	0.00454	70%	0.02084
			30%	0.01607		
P5	65	1.5 cm right	15%	0.032	60%	0.248

The vertical coil location was always 2 cm above the inion for all participants.

the optimum value, the effect of a randomness of the noise becomes strong and the output impulse train becomes disordered. In other words, the signal-to-noise ratio (SNR), or signal detection sensitivity, is highest at the optimum noise intensity.

According to the SR theory, the dependency of contrast threshold (C_{th}) for the discrimination of stimulus orientation on noise intensity can be described by the following equation:

$$c_{th} = \frac{K_1\sigma}{\Delta}\exp\left[\Delta^2 / \left(2\sigma^2\right)\right] \tag{2}$$

where K_1 is an adjustable constant, Δ is a threshold value in signal transmission and σ is a r.m.s. noise intensity. This equation was derived from a threshold SR theory (Simonotto et al., 1997). We should notice that Simonotto et al. used constant artificial threshold, thus they K_1/Δ constant K. We replaced σ by $K_2\ \sigma_{TMS}$ to use TMS intensity as the noise intensity. K_2 is a transformation coefficient of the value of TMS intensity related to the participant's threshold for the non-TMS condition for each participant. There is always internal noise in a real system. Therefore, the noise in SR phenomena includes the sum of the external noise, which is generated by TMS in our case, and the internal one. However, it is very difficult to measure actual internal noise intensity, and it is expected to be small. Thus, we treated the TMS intensity (σ_{TMS}) as the noise intensity. We used the individual non-TMS threshold as the threshold Δ instead of an artificial threshold used by Simonotto et al. Then the final equation is as follows:

$$C_{th} = \frac{K_1'\sigma_{TMS}}{\Delta}\exp\left[\Delta^2 / \left(2K_2^2\sigma_{TMS}^2\right)\right] \tag{3}$$

where $K_1' = K_1\ K_2$ and σ_{TMS} » internal noise.

Fig. 3 shows the experimental data of Fig. 2 (filled circle) and the fitted curve for C_{th} as a function of σ_{TMS} (noise intensity) as a continuous line. Parameter values of the fitted curves in Eq. (3) are listed in Table 3. Eq. (3) gave an approximate fit for the psychophysical data of all participants, with the exception of P5. However, TMS intensity at the minimum C_{th} value of participant P5 agrees with the value obtained according to the SR theory (Fig. 3e). Differences in the values of K_1' and K_2 among participants did not appear to be large, as shown in Fig. 3f. The experimental threshold value near zero noise intensity does not agree with the theoretical one. This is probably due to the fact that the SR theory definition dose not explicitly include internal noise, although neural systems always have some internal noises (Wiesenfeld and Moss, 1995; Moss et al., 2004). SR theory is one of the theories used to calculate the signal-to-noise ratio in the presence of a sub-threshold signal and noise simultaneously. Hence, a theoretical signal-to-noise ratio diverges from experimental results when the noise is close to zero as shown in Fig. 3 a - e. In reality, however, such a situation does not have a meaning, because amplitude of signal plus noise cannot be over the threshold of the SR model (not to be confused with human contrast threshold). Therefore, the SR theory at its basic form does not apply when TMS noise is close to zero. An SR model that would produce a good fit to the results at low TMS values is out of the scope of the current paper, since we do not know what kind of noise TMS produces at the cortex and how it interacts with internal neural noise. Our results indicate that C_{th} versus σ_{TMS} shows close qualitative agreement with the SR theory as a threshold device. This result clearly supports the view that an SR kind of phenomenon occurs in the human brain.

4. Discussion

We measured human pattern discrimination performance as a function of the intensity of transcranial magnetic stimulation (TMS) to the early visual cortex (V1/V2). The timing and location were varied in order to search for the maximum effects. Our results demonstrate that a stochastic resonance (SR) kind of phenomenon is observed in the human cortical visual system when the TMS timing and location are suitable. Enhancement of performance in an orientation discrimination task reached its maximum at a TMS intensity of approximately 30% of the maximum and, thereafter, plummeted to negative values. The optimum SOA was around 60 ms and the optimum coil location was 2 cm above the inion and within 1.5 cm on the right-hand side, where TMS stimulated the early visual cortex. At other nearby locations, TMS did not have any effect. The characteristics of performance in the presence of noise are consistent with the SR theory based on a threshold device model (Jung, 1994; Gingl et al., 1995). These suggest that a cortical threshold mechanism exists at V1 or at a higher level in the ventral stream.

SR phenomenon in threshold systems is based on the assumption that a frequency spectrum of the adding noise is white or a colored with a limited bandwidth (Gingl et al., 1995). In general, a continuous white noise is used in SR experiments. On the other hand, the output from the magnetic stimulator is pulsed and not continuous. By the way, in TMS, the duration of the induced current is short, about 100 μs, and thus can be regarded as an impulse. Theoretically, the frequency spectrum of the impulse is white and has no correlation with anything other than itself. Thus, TMS acts as an independent noise that does not correlate with on-going neural activity. In addition, consistency of the SR characteristics between the SR theory and ours strongly supports that TMS acts as a noise as required by SR phenomena.

TMS produces a loud click and induces scalp muscle contraction, and, thus, evokes response to multisensory stimuli. One might think that

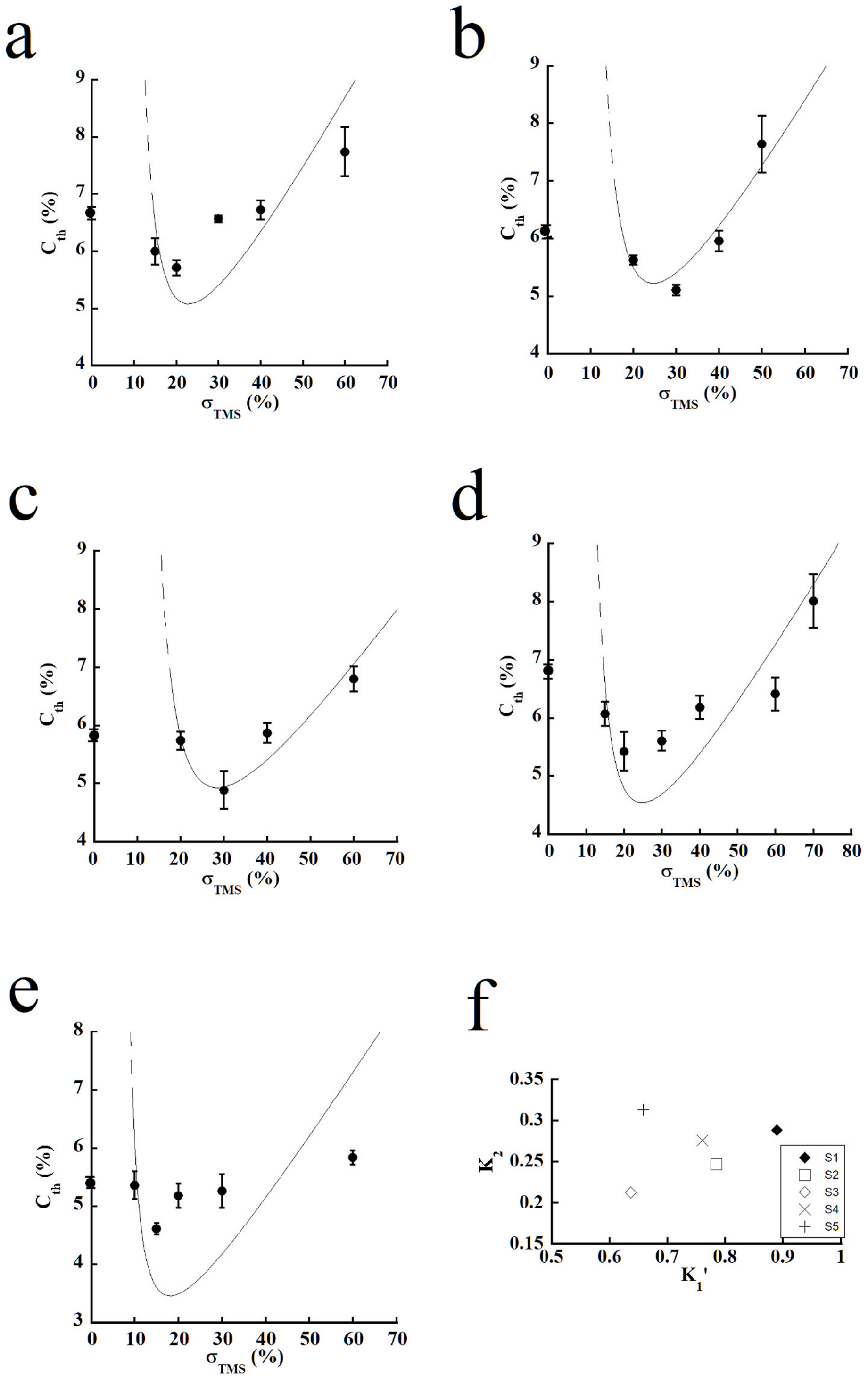

Fig. 3. Contrast discrimination threshold (C_{th}) versus noise intensity (σ_{TMS})

The participant, coil position, and SOA from (a) to (e) are the same as those of (b), (d), (f), (h) and (j) of Fig. 2, respectively. The threshold ($\varDelta$) values were as follows: (a) participant P1: $\varDelta$ = 0.0659; (b) participant P2: $\varDelta$ = 0.0608; (c) participant P3: $\varDelta$ = 0.0590; (d) participant P4: $\varDelta$ = 0.0683; (e) participant P5: $\varDelta$ = 0.0534; and (f) parameter values K_1' and K_2. C_{th} is Weber contrast whose unit is percentage, and σ_{TMS} is TMS intensity to maximum output, whose unit is also percentage. The solid lines in (a) to (e) represent the best fit obtained from Eq. (3) with the parameters which are plotted in (f). The dashed lines represent the portion where Eq. (3) is not applicable due to small TMS intensity. The error bar represents ± SE.

Table 3
Parameter values of the fitted curves in Eq. (3).

Participant	threshold value ($\varDelta$)	K_1'	K_2
P1	0.0659	0.88961	0.28852
P2	0.0608	0.78432	0.24733
P3	0.0590	0.63622	0.21264
P4	0.0683	0.76078	0.27611
P5	0.0534	0.65793	0.31333

such non-specific effects of TMS, might facilitate visual discrimination at low intensities. However, no enhancement was observed when the SOA or the coil position was different from that at which SR was observed. Twenty-millisecond difference in SOA or 0.5 cm displacement in coil position did not induce any SR effects. If TMS-associated non-specific-effects had induced the SR phenomenon, it could have been observed under almost all conditions in our experiments. Moreover, the click-sound-experiment did not show a statistically significant difference in the thresholds between presence and absence of click sound. Therefore, our results demonstrate that the SR we observed is a specific effect of TMS.

Our coil was located 2 cm above the inion and at a distance of 0–2 cm towards the right side. Recent studies have reported that such a TMS coil location stimulates both V1 and V2; however, there is a significant variation between participants (Kammer et al., 2005; Thielscher et al., 2010; Salminen-Vaparanta et al., 2012). Hence, it is difficult to determine an accurate area to be stimulated using anatomical landmarks alone without the utilization of neuronavigation.

It has been reported that the arrival time of visual stimuli to V1 is 55–70 ms by analyzing neuromagnetic signals (Vanni et al., 2001), and 50–80 ms by a combination of visual evoked potentials and functional magnetic resonance imaging (Vanni et al., 2004). This arrival time is in good agreement with our result (59 ms). Romei et al. (2007) reported effects of TMS on the reaction time (RT) to detect visual stimulus. TMS was applied to the occipital pole at 70% intensity and SOA 30–150 ms. We can know an arrival time of the stimulus to V1 cortex by measuring TMS-effect on RTs. When the RT varies from the control (without TMS), the applied SOA refers to the arrival time of the stimulus. Measured RTs in the SOA range of 60–75 ms were longer than in the control. This result is in good agreement with ours, SOA was around 60 ms. These agreements strongly support that observed SR phenomenon occurred in the early visual cortex. Therefore, enhancement seems to occur at an initial stage of visual information processing in the brain. The chronometry of visual processing is very complicated; thus, further investigations are needed (de Graaf et al., 2014). Our results indicate that observed SR kind of behavior can be explained by the threshold SR theory (Jung, 1994; Gingl et al., 1995). Substantiation of the SR theory by our results indicates that TMS acts as random neural noise in the initial processing stage leading to figure discrimination. Figure recognition (identification) is more likely to occur in the infero-temporal cortex rather than in the early visual cortex (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992; Merigan and Maunsell, 1993). Considering the results of the current study and those of Simonotto et al. (1997), it is reasonable that SR occurs in the early visual cortex, because that cortex mediates the signal to higher processing areas, such as the infero-temporal cortex (see section 4.1).

In our experiment, the number of participants was not large, thus it should be considered as a psychophysics study. We measured the figure discrimination threshold, which is a psychological quantity. It needs to consider inter-participants differences to such quantity. We examined whether SR phenomena occur in the discrimination performance, and whether SR characteristics of performance are consistent with SR theory for each participant. In a small sample size study, we need to pay attention to sampling artifacts. Four of five participants, however, show good SR profiles as shown in Figs. 2 and 3. In addition, no significant differences across participants were found in coil position, SOA, and TMS intensity when SR occurred. Therefore, we believe that sampling artifacts are negligible, although the sample size is small.

Simonotto et al. (1997) demonstrated the SR phenomenon of performance in contrast detection task. They analyzed human data using the SR theory based on a threshold device, and showed consistent with that theory. Abrahamyan et al. studied the effects of low intensity TMS on a visual signal detection task (Abrahamyan et al., 2011), and an orientation discrimination task (Abrahamyan et al., 2015). TMS on contrast detection, found an optimum SOA of 100 or 120 ms in the detection, and an optimum SOA of 106 ms in the discrimination task. The clearly longer SOAs than ours probably mean that they were stimulating a higher processing level area than in our study, in which the SOA was about 60 ms. This suggests that an SR kind of effect can occur at different locations at the visual cortex. If this proposition is correct, it is interesting that what kinds of SR phenomena do occur in higher level process, when and which sub-area do those phenomena occur, and what kind of differences do those phenomena show between used tasks. They pointed out that observed enhancement was a result of the pedestal effect (see Legge and Foley, 1980). Schwarzkopf et al. (2011) observed an improvement of motion discrimination at low TMS intensity for low motion coherence stimuli. This was one of the SR phenomena observed at a higher processing level than targeted in our study. They used triple-pulse TMS, therefore the timing of the SR phenomenon was not accurate. On the contrary, different results were reported for high motion coherence stimuli; no improvement in the discrimination for high coherence stimuli was reported. The difference was explained by the adapted state or the suppressed state of the stimulated area. Van der Groen and Wenderoth (2016) used transcranial random noise (tRNS, which is randomly alternating electrical current) to stimulate the occipital region of participants. They found that the detection accuracy of participants first increased and then decreased as the current increased. This was similar to the case when visual noise was added to the stimulus images without tRNS. This, however, only happened when stimulus contrast without noise was adjusted to produce 60% of correct responses. When an 80% accuracy was used, there was no effect of noise. The 60% accuracy corresponds to lower contrast than the 80% accuracy. The above results show that the SR phenomenon only occur in suitable experimental and stimulus condition.

4.1. Similarity of the SR characteristics

Wiesenfeld et al. (1995) and Simonotto et al. (1997) have analyzed observed SR phenomena by using the SR theory, to the best of our knowledge. The former study was on the excitability of single neurons in crayfish mechanoreceptors and the latter was on contrast detection thresholds. The analytical results were in fairly good agreement with the SR theory. Three results, including ours, agree with the general formula (1) of the underlying the SR phenomenon. Tasks used in these three studies were different, thus one would expect that the SR characteristics of each experiment would be different from each other, but this was not the case. We believe that the followings are reasons for this similarity of the SR characteristics. First, we look to consistency of the contrast detection threshold. Visual information in the brain is produced through the following process. An image from the eye is first reached V1, and detected each of the various small elements. Information is gradually transmitted to higher-order areas for integration and recognition. The neural networks involved in the integration process are used in different ways for different tasks. Recognition results vary depending on what we focus on, even for the same image. However, if noise is added to V1 at the same time as processing starts in V1, processing image would be equivalent to that of a noise contaminated image. In our study, the SR phenomenon was observed in the early visual cortex (V1/V2) at a SOA of around 60 ms. This condition is the time when the information from the eye reaches V1, as shown by Vanni et al. (2001, 2004) and Romei et al. (2007). Figure recognition (identification) is more likely to occur in the infero-temporal cortex rather than in the early visual cortex. However, information processed at lower level is treated in higher level processing. Therefore, enhancement of contrast detection leads that of discrimination. It is reasonable to conclude that our SR phenomenon occurs in the early visual cortex.

Next, we consider the consistency of the SR characteristics between figure discrimination and activity of single neurons. It is well known that synchronization of neural activity occurs in the brain during cognition (Usrey and Reid, 1999; Ward, 2003; Uhlhaas et al., 2009; Grover et al., 2021). In addition, Kitajo et al. (2007) and Ward et al. (2010) found large-scale synchronization of neural activity, which was mediated by the SR phenomenon. Those were conducted for contrast detection and sound detection, respectively. In order to occur synchronization between different cortical regions, each property of neural networks in those regions must be close each other. If they are considerably different, it is not easy to synchronize. This suggests that properties of the neural activity involved in contrast detection can be similar to that of single neurons. In this case, we cannot know for sure, but it is possible that the synchronization of neural activity was done in a way that aligned with single neurons, which is the most basic component unit of the neural system. There are various types of synchronization and frequency bands, however, the details are still unknown (Uhlhaas et al., 2009; Grover et al., 2021).

4.2. Stochastic resonance vs non-linear transducer

Both SR theory and the pedestal effect focus on the nonlinearity of the system. There are several types of SR theories, they are all built on fairly well-defined physical models (Wiesenfeld and Moss, 1995; Gammaitoni et al., 1998). In the SR theory based on a threshold device model, the device acts as a level-crossing detector, i.e. subthreshold signal is detected by adding optimal amount of noise to exceed a threshold. On the other hand, an origin of the pedestal effect was a non-linear transducer model proposed by Legge and Foley (1980) to explain the so-called dipper-shaped curve of contrast discrimination as s function of pedestal contrast of sinusoidal gratings. As Abrahamyan et al. discussed, adding noise to the input signal is equivalent to adding up an input level of the signal (i.e. a pedestal) by a comparable amount of noise. Therefore, as noise increases, a threshold value decreases to a minimum and then returns to an original value. The idea of the pedestal effect is equivalent to the threshold device model of SR, and consistent with the results of Goris et al. (2008). In relation to the nervous system, the form of the nonlinearity can be clearer for the SR theory based on a threshold model than for the pedestal effect.

5. Conclusions

In this study, we investigated the so-called SR phenomenon, in which the discrimination accuracy first improves and then decreases with increasing noise intensity when direct noise is applied to the visual cortex during figure discrimination. We found that an SR kind of phenomenon can be produced by stimulating the early visual cortex (V1/V2) at about 60 ms after the presentation of visual stimuli, and the SR characteristics were in line with the SR theory expressed in a threshold device model. The SR characteristics in figure orientation discrimination were similar to other SR phenomena observed in different neural processing stages such as single sensory neurons and contrast detection.

Author contributions

Yamazaki H.: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. Pantelis L.: Methodology, Investigation, Writing – review & editing.

Acknowledgments

This work was partly supported by a grant from Computer Science Laboratory, Fukuoka Institute of Technology. We would like to thank our participants for their cooperation. We also thank Docent J. P. Mäkelä for the generous support and many helpful discussions.

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