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TMS-induced motor activation increases visual awareness

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Abstract

The influence of non-perceptual information on visual awareness has recently gained substantial interest. Here, we investigated a potential contribution of evidence from the motor system to visual awareness ratings using single-pulse Transcranial Magnetic Stimulation (sp-TMS). We hypothesized that TMS-induced activation of motor cortex will increase the subjective awareness ratings as compared to sham stimulation. Additionally, we investigated whether TMS-induced motor evoked potentials (MEPs) could be treated as a measure of evidence accumulation resulting in behavioral response. Participants performed a visual identification task and rated their subjective experience with Perceptual Awareness Scale (PAS). During the task, we delivered sp-TMS and recorded MEPs with EMG placed on participants hand. Delivering sp-TMS to primary motor cortex resulted in higher average PAS ratings as compared to the control condition, but only in trials where stimulation was congruent with the response performed. Additionally, reaction times in the identification task were also higher in congruent trials. MEP amplitudes correlated with PAS ratings when response congruence was taken into account. We argue that activity in motor cortex influences visual awareness of the participants. Subsequently, MEP might serve as an indirect measure of both perceptual and non-perceptual evidence accumulated for visual awareness ratings. Finally, we conclude that the integration of additional information results in prolonged RTs in the identification task. Our results suggest that task-related motor activity influences visual awareness, extending the classical view on how visual awareness is shaped.

Keywords: Awareness ratings, Identification task, Motor cortex, Motor Evoked Potential, Transcranial Magnetic Stimulation, Visual perception

Abbreviations: PFC, prefrontal cortex; dlPFC, dorso-lateral prefrontal cortex; CI, confidence interval; CS, confidence scale; EMG, electromyography; FDI, first dorsal interosseous; M1, primary motor cortex; MEP, motor evoked potential; MSO, maximal stimulator output; PAS, perceptual awareness scale; PPC, posterior parietal cortex; PMd, dorsal premotor cortex; RMT, resting motor threshold; RT, reaction time; sp-TMS, single-pulse TMS; SD, standard deviation; SE, standard error; TMS, transcranial magnetic stimulation.

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1. Introduction

Uncovering the cognitive and neural mechanisms of visual awareness can be considered a central problem in consciousness science, as the majority of its research is conducted in that modality (Faivre et al., 2017). Despite this cumulative scientific effort, most influential theories offer divergent approaches to solving the problem (e.g. Dehaene et al., 2014; Lamme, 2010; Lau & Rosenthal, 2011; Tononi et al., 2016). Their proponents have opposing views not only on the underlying mechanisms but also can differ substantially concerning which aspects of conscious processes should be considered as visual awareness. Therefore to avoid potential ambiguity, we start by explicitly limiting the understanding of the term visual awareness in this paper to conscious access to visual information. This approach is consistent with several major theories of consciousness, including the hierarchical view (Lau & Rosenthal, 2011) or Global Workspace Theory (Dehaene & Changeux, 2011), and allows treating various subjective scales, such as PAS (Ramsøy & Overgaard, 2004) or Confidence Rating (CR, Dienes & Perner, 2004) as measures of visual awareness.

Majority of consciousness theories frame visual awareness predominantly in the context of processing perceptual evidence (Block, 2011; Dehaene et al., 2003; Lamme, 2010). This has strongly bounded research to paradigms manipulating only the characteristics of stimuli. However, the strength and physical qualities of stimuli cannot fully explain the variability of visual awareness observed in experiments, which implies there might be additional non-perceptual sources of influence (Anzulewicz & Wierzchoń, 2018). Recent research identified several such factors, e.g. prior expectations held by participants (Snyder et al., 2015), their previous responses (Rahnev et al., 2015), or influence of attention (Fazekas & Overgaard, 2018). Nevertheless, this approach focuses only on the impact of initial conditions preceding visual stimulation on its subsequent processing and some theories acknowledge this contributing role of the state of the cognitive system on visual awareness (e.g. Dehaene et al., 2014). In this paper, we investigated factors that could influence visual awareness and come into play after the presentation of the stimulus.

From many potential contributors, the motor system seems especially related to perception. There is a large body of research exploring the action-perception loop, showing that in tasks requiring coordination of perceptual information and action, both systems influence each other leading to performance improvement (Donnarumma et al., 2017; Hecht et al., 2001). A similar effect can be observed in experiments, where the coupling between perception and action is more superficial than in action-perception loop procedures (e.g. with mapping certain stimuli to particular response keys). Our recent study showed that awareness ratings were affected by performance monitoring (Siedlecka et al., 2019). Participants reported lower awareness if their response in the previous trial was incorrect. Moreover, this effect was stronger when accuracy feedback was introduced after every trial.

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Influence of action on visual awareness in these paradigms is generally interpreted in terms of proactive tuning of the perceptual system, exhibited in subsequent trials of a task.

Nevertheless, recent research suggests there might be a more immediate effect that shapes the experience of just seen stimuli. In a series of experiments, it was shown there is a consistent effect of response order where perceptual scale ratings are altered by the behavioral response to the identification task appearing before or after the scale (Siedlecka et al., 2016; Wierzchoń et al., 2014). This effect was interpreted in the context of evidence accumulation, where performing a motor response to an identification task acted as an additional portion of evidence for assessment of the response congruence with the stimulus.

Anzulewicz et al. (2019) argue that there are at least four potential mechanisms through which action planning or execution could influence visual awareness. They point to possible indirect effects that stem from motor activity affecting other cognitive processes like engagement of attentional resources, restricting the number of available alternatives in the decision process or enhancing performance monitoring (as it seems to be the case in Siedlecka et al., 2019). The fourth possibility refers to a direct influence that action can have on shaping visual awareness through providing additional non-perceptual information that is integrated into visual awareness by evidence accumulation processes.

Evidence accumulation is strongly coupled with the presence of stimulation but continues to process information at least to the moment one decides about the stimulus which typically is manifested by behavioral response (Yeung & Summerfield, 2012). During this time perceptual information is processed by sensory areas, but it also exposes an opportunity for non-perceptual information to influence the formation of visual awareness. This seems to be the case in a study of Gajdos et al. (2019), where authors observed higher subjective ratings in trials where partial muscular activation followed stimulus presentation but preceded behavioral response. They argue that such activity could have contributed as additional evidence while being unrelated to the task itself (there was no effect on behavioral accuracy). However, due to the paradigm design, this relation is only correlational and does not allow the exclusion of other possibilities.

This ambiguity could be resolved through the explicit introduction of additional motor activation unrelated to the main task. In our recent paper (Siedlecka et al., 2019) we achieved that with a second task that participants had to perform between stimulus presentation and stimulus-related responses that shared the same response code. Performing additional motor response congruent with the response scheme of the main task increased participants visual awareness ratings. Subsequently, congruence with the correct response in a given trial did not have any influence. On top of that, there was no effect of performing a motor response unrelated to the main task response scheme. These results were interpreted in the context of evidence accumulation mechanisms, where overlapping responses would increase the amount of evidence (either for or against a particular response), while

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other types of motor activity could not be used as evidence for visual awareness. This experiment provides arguments for directional interpretation of the relation between motor activity and visual awareness. However, it cannot be ruled out that additional task itself or the additional visual information from the displayed cue could be responsible for the observed effects.

Proper assessment of the selective effect of motor information on visual awareness would require alternating the activity of motor cortex directly. Recently Fleming et al. (2015) attempted this through non-invasive brain stimulation with TMS. Their results showed that sp-TMS protocol applied to PMd but not M1 associated with the unchosen response reduced confidence and in consequence decreased metacognitive sensitivity without influencing identification performance. The effects of sp-TMS on confidence were observed for pulses applied both before and after the participants' identification response, suggesting that confidence depends on processes lasting even after the decision has been made. The effect on metacognitive sensitivity, on the other hand, was present only in pre-response condition. Authors conclude that only PMd activation contributes to subjective ratings. However, on the contrary, the previously mentioned study (Siedlecka et al., 2019), their manipulation did not produce additional behavior since the stimulation was set below participants AMT and did not evoke motor responses. Subsequently, sp-TMS was delivered in close proximity to the behavioral response, which might have obscure its effect.

Considering the limitations of previous research, in the current study we investigated whether externally introduced motor-related information can be integrated into visual awareness ratings while being separated from the behavioral response. To achieve this, we modified the methodology of Fleming et al. (2015) and delivered sp-TMS pulses above RMT to M1 involved in generating behavioral responses in the experimental task. Moreover, we separated the sp-TMS and the behavioral response with subjective scale reported verbally to minimize the interference of intentional motor activity with that evoked by the sp-TMS. Based on our previous findings, we expected to observe an effect of stimulation on visual awareness ratings in the M1 condition as compared to the control condition. Subsequently, we investigated the effect of congruence of stimulation with either the stimulus or the participants' response (similarly to Gajdos et al., 2019).

To actively control the precision of sp-TMS pulse delivery, we employed an EMG coupled with the stimulator and recorded muscle activity (MEPs) on the response finger contralateral to the stimulation side. Previous research on MEP has shown, that its amplitude can reflect the level of excitability in respective M1 area (Fitzgerald et al., 2002). Subsequently, it has been established that motor imagery of unilateral movements is associated with increased excitability of a highly specific representation in the contralateral M1 (Facchini et al., 2002; Fourkas et al., 2006; Jeannerod, 1995). Based on that, we expected this excitability to be influenced by the preparatory motor plan for the subsequent identification task response. Therefore, we hypothesized that processes of evidence accumulation could influence the strength of preparatory motor plan and through subsequent changes in the excitability of M1 be reflected in MEP amplitude (the more the evidence, the higher MEP amplitude). If

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that would be correct, then we would expect differences in MEP amplitude between trials with different visual awareness ratings.

2. Materials and methods

The experiment was carried out in the TMS Laboratory of the Institute of Psychology, Jagiellonian University, placed at the Neurology Clinic of University Hospital. The study was approved by the ethics committee of the Institute of Psychology at Jagiellonian University and carried out in accordance with the approved guidelines for TMS (Rossi et al., 2009; Rossini et al., 2015) and the Declaration of Helsinki (Holm, 2019).

2.1 Participants

Healthy volunteers meeting the criteria for participation in TMS studies (no history of neurological disorders, psychiatric disorders, or head injury etc. as assessed by safety screening questionnaire) were recruited via the internet. One participant resigned from the experiment due to TMS-induced headache, while forty-six participants (eleven males, M_{age} = 23.2, range = 19-37) completed the study. All participants had normal or corrected to normal vision. They were informed about the general purpose of the experiment, and that they could withdraw at any time without providing a reason. Prior to the experiment, participants completed a safety screening questionnaire and signed an informed consent form. After the experiment, they received monetary compensation (160 PLN).

2.2 Session sequence

The experiment was conducted on a computer in a within-subject design and consisted of one session. Participants completed the training (15 trials, ~2 min) for the identification task where objective response preceded reports of subjective awareness using the PAS (Ramsøy & Overgaard, 2004; Sandberg et al., 2010). Then a staircase procedure was used to estimate the stimulus contrast that would lead to about 79% of correct responses. The median contrast for each PAS rating was calculated using a 1-up-3-down staircase (100 trials; stair size 0.005, starting with 0.09; ~5 min).

Subsequently, individual RMTs were determined and participants completed 32-trial training that was identical to the experimental procedure (subjective report followed by objective response, sp-TMS pulses to the left M1). Finally, they completed the experimental task consisting of two conditions in four counterbalanced blocks (two experimental and two control). Simultaneously, EMG signal was recorded from the FDI muscle of the right index finger. Each block consisted of 100 trials which summed up to 400 trials for the whole experiment and took about 45 minutes to complete.

2.3 Stimuli and procedure

The task was coded in PsychoPy software (Peirce, 2007) and run on a PC. Participants placed their heads on a chinrest mounted 60 cm away from the LCD monitor (1920 x 1080 resolution, 59 Hz

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refresh rate). Stimuli consisted of Gabor patches tilted left or right (-45 or 45 degrees rotation from vertical angle respectively) presented centrally on the screen (128 x 128 pixels, which translated to 3.2 degrees of visual angle). Visibility of the stimulus was manipulated through a white noise patch of variable contrast placed on top of the stimulus. Figure 1 outlines the temporal organization of an experimental trial. Participants did not receive any feedback about their performance.

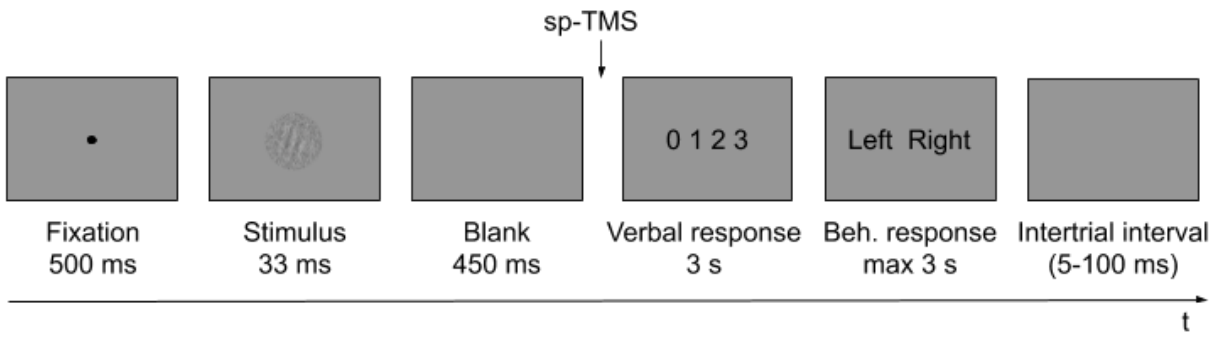

Fig. 1. Schematic illustration of an experimental trial. First, a fixation dot was presented for 500 ms. A Gabor patch masked with white noise was then displayed for 33 ms, followed by an empty screen shown for 450 ms. Subsequently, an sp-TMS pulse was administered and a screen prompting the subjective rating was displayed for 3 seconds or until a verbal rating was provided using PAS (with the points of the scale defined as 0 = no experience; 1 = a brief glimpse; 2 = almost clear experience; 3 = clear experience). It was followed by a screen prompting a motor response to the objective task was also displayed for 3 seconds or until a keyboard button press was made (either "Z" with the left index finger or "M" with the right one). Trials were separated with an intertrial interval of variable length.

2.4 sp-TMS parameters

Biphasic sp-TMS was delivered with a Magstim Super Rapid[2] Plus[1] stimulator, using a 70 mm Double Air Film Coil at 110% of the individual RMT (average intensity = 65.87%, SD = 10.67, of the MSO). The individual RMT estimation started from applying sp-TMS at 50% of MSO to the left M1. Then, by varying stimulation intensity, a site where suprathreshold sp-TMS induced the maximal twitch in the right index FDI muscle was established. Afterwards, the lowest intensity that resulted in the MEPs larger than 50μV peak-to-peak amplitude on five out of ten consecutive trials was determined. Stimulation in the control condition was administered to the interhemispheric cleft, between the postcentral gyri, with the handle pointing backwards. The site of stimulation and tangential position of the coil to the scalp was monitored using the average brain template in Brainsight 2.3 neuronavigation system. For the M1 stimulation, the current in the brain was PA-AP and the main axis of the coil was oriented at 45° offset from the posterior-anterior (PA) direction. For the control condition, the coil was not tilted. During sp-TMS, participants wore earplugs for noise protection.

2.5 Data analysis

We used linear logistic regression mixed models with separate intercepts and slopes parameterization to improve readability of regression coefficients. The conditions in the experiment were defined by the

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congruence with the sp-TMS of either the stimulus (stimulus-congruent, stimulus-incongruent) or the response (response-congruent, response-incongruent). The following parameters were compared within the conditions: identification task accuracy, identification task RT, visual awareness ratings (mean PAS rating), and MEP amplitude. The models were fitted using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) in the R Statistical Environment. Additionally, we used lmerTest package (Kuznetsova et al., 2017) for calculating p-values of estimates, phia (De Rosario-Martinez, 2015) and emmeans packages (Lenth, 2019) for pairwise comparisons, and metaSDT package (Craddock, 2019) for calculating metacognitive efficiency.[1] For MEP-related calculations, we followed common practice from literature and only used trials with MEP > 50 μV peak-to-peak amplitude. Throughout the analyses α level was set at 5%.

For each analysis we run identical models, swapping only stimulus and response congruence as predictors, and compared them to identify which one has the best fit (based on AIC, BIC and Log-Likelihood measures). Here we report only the models with the best fit. Additional pairwise comparisons of simple effects were corrected with Tukey method performing family-wise error rate correction.

3. Results

3.1 PAS ratings

In the first step, we wanted to assess if data from subjective ratings is better explained by congruence with presented stimulus or response performed. In our experimental design, those two factors are strongly intertwined, because of overall high accuracy forced by the staircase procedure (correct trials have stimulus and response congruence matched). However, in incorrect trials, stimulus and response congruence have to be opposite. Therefore, we fitted a mixed linear model to PAS ratings data only for incorrect responses and found a significant interaction between condition and response congruence ($t(3078) = 2.79$, $p = .005$). Further pairwise analysis of simple effects revealed that PAS ratings for congruent stimuli in the M1 condition were higher than for the control condition (z ratio = 3.40, $p = .004$). This mirrors the effect found in correct trials: interaction of condition and response congruence ($t(14752) = 2.87$, $p = .004$), and simple effect of condition for congruent responses (z ratio = 3.53, $p = .002$). Based on these results, we treated response congruence as explaining the data better than stimulus congruence and used it as a factor in all subsequent analysis.

Proper assessment of the relation between factors of interest and PAS ratings was done on full data (both correct and incorrect). We fitted a linear mixed-effect model with condition and response congruence as fixed effects, random slopes for response congruence, and subject-specific intercepts. Here also we did not find an effect of condition or congruence alone, but there was a significant

[1] The raw data and the scripts for analyses are available at https://osf.io/29n6j.

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interaction between the two factors (*t(17879)* = 2.37, *p* = .018, see Table 1 for all estimates). Pairwise comparisons indicated a significantly higher mean PAS rating in M1 compared to the control condition, but only for congruent stimuli (*z* ratio = -3.11, *p* = .010).

Table 1. Linear mixed-effect model for PAS ratings with condition and response congruence as fixed effects, and random subject-specific intercepts response congruence effects.

	Estimate	**Std. Error**	***t* (df)**	***p***
(Intercept)	1.2930	0.0691	18.710 (46.3)	< 2e-16
Condition	- 0.0088	0.0165	- 0.534 (17882.8)	.593
Response congruence	- 0.0011	0.0425	- 0.027 (52.5)	.979
Condition x Resp. Congruence	**0.0652**	**0.0234**	**2.786 (17879.0)**	**.005 ****

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

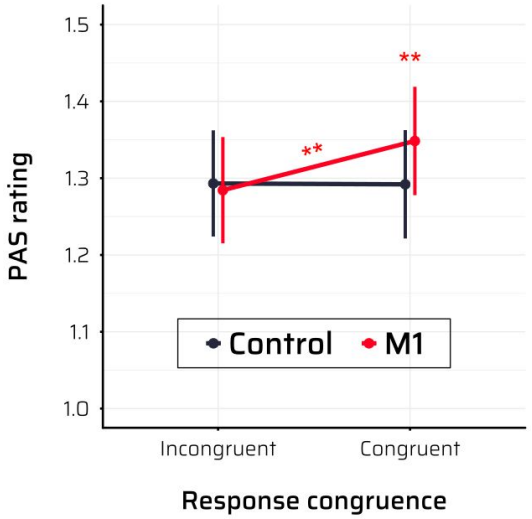

Fig. 2. PAS ratings as a function of the response congruence and the TMS condition. Error bars represent SEs.

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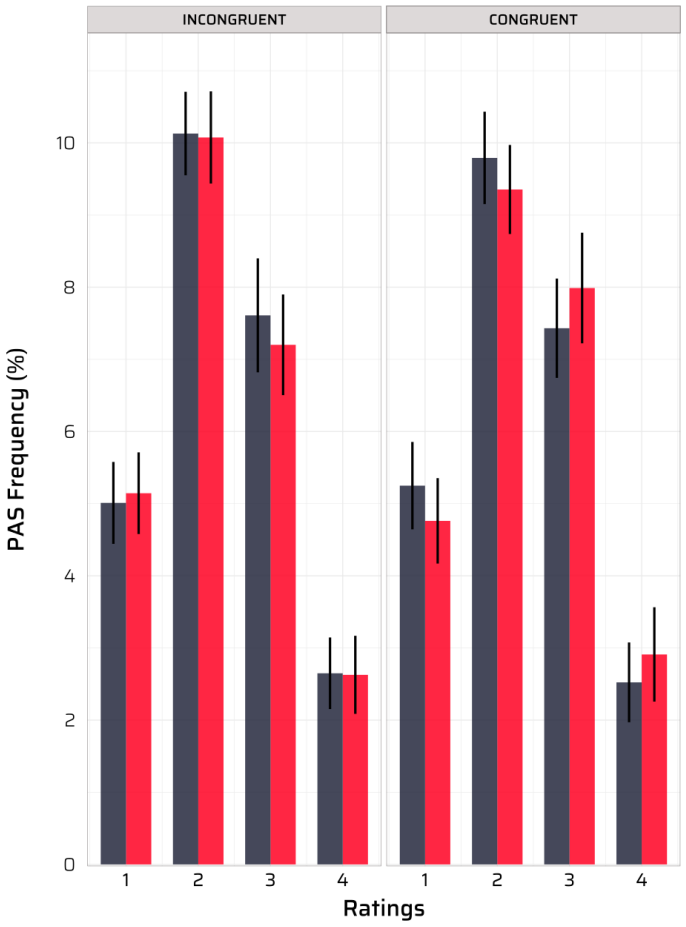

Fig. 3. PAS ratings frequencies depending on response sp-TMS-congruence. Error bars represent SEs.

3.2 Task accuracy

We fitted logistic mixed-effect model with condition and response congruence as fixed effects, random slopes for response congruence, and subject-specific intercepts. We found no significant differences in identification task accuracy (see Figure 2), between congruent and incongruent trials (z = 0.41, p = .683), or between control and stimulation conditions (z = 0.07, p = .947). Table 2 contains all estimates from the model.

Table 2. Logistic mixed-effect model for accuracy with condition and response congruence as fixed effects, subject-specific intercepts and random slopes for response congruence.

	Estimate	**Std. Error**	***z***	***p***
(Intercept)	1.7251	0.1121	13.377	< 2e-16
Condition	0.0378	0.0569	0.067	.947
Response congruence	0.0510	0.1247	0.409	.683
Condition x Resp. congruence	- 0.0321	0.0810	- 0.396	.692

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Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

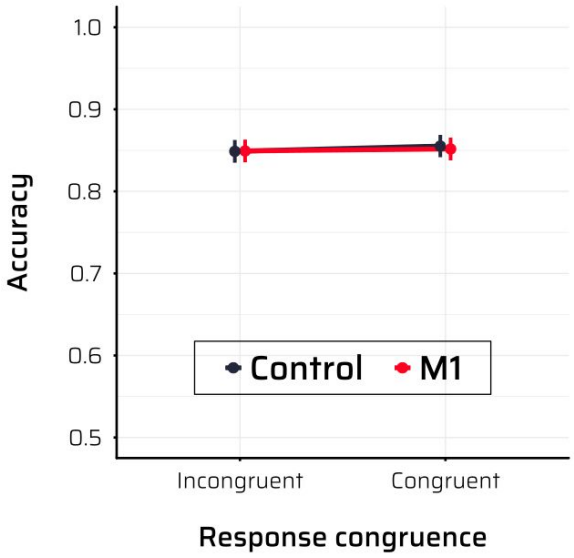

Fig. 4. Identification task accuracy as a function of the stimulus congruence and the TMS condition.

3.3 Reaction times

We fitted a linear mixed-effect model with condition, response congruence, and PAS ratings as fixed effects, random slopes for response congruence, and subject-specific intercepts. We found a significant interaction between condition and response congruence ($t(17888) = 2.05$, $p = .040$). Further investigation revealed that response times in congruent condition with stimulation of M1 were significantly different from other conditions (see Table 3 for pairwise comparisons). Additionally, we were interested in the differences between the M1 and control condition for congruent trials were statistically different for each PAS rating. Conditional pairwise comparisons revealed that for 0, 1 and 2 rating RTs were significantly bigger (see Table 4 for pairwise comparisons of interest).

Table 3. Pairwise comparisons of simple effects for the interaction of condition and response congruency factors. Trials in the M1 condition and congruent response were significantly different from all other types of trials.

			Estimate	Std. Error	*z* ratio	*p*
Control, incongruent	–	M1, incongruent	-0.00431	0.00452	-0.953	.7763
Control, incongruent	–	M1, congruent	**-0.02406**	**0.00619**	**-3.884**	**.0006*** **
Control, incongruent	–	Control, congruent	-0.00663	0.00623	-1.063	.7120
M1, incongruent	–	Control, incongruent	-0.00232	0.00624	-0.372	.9824
M1, incongruent	–	M1, congruent	**-0.01975**	**0.00620**	**-3.186**	**.0079** **
Control, congruent	–	M1, congruent	**-0.01743**	**0.00452**	**-3.859**	**.0007*** **

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Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Table 4. Pairwise comparisons of regression coefficients for the linear regression model in congruent trials between control and the M1 condition for each PAS rating. Conditions differed significantly for the PAS rating 1 and 2.

Control, congruent – M1, congruent	**Estimate**	**Std. Error**	***z* ratio**	***p***
PAS 0	-0.021337	0.00913	-2.337	.0897 ·
PAS 1	**-0.023063**	**0.00647**	**-3.563**	**.0021****
PAS 2	**-0.024906**	**0.00734**	**-3.393**	**.0039****
PAS 3	-0.000412	0.01216	-0.034	1.0000

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

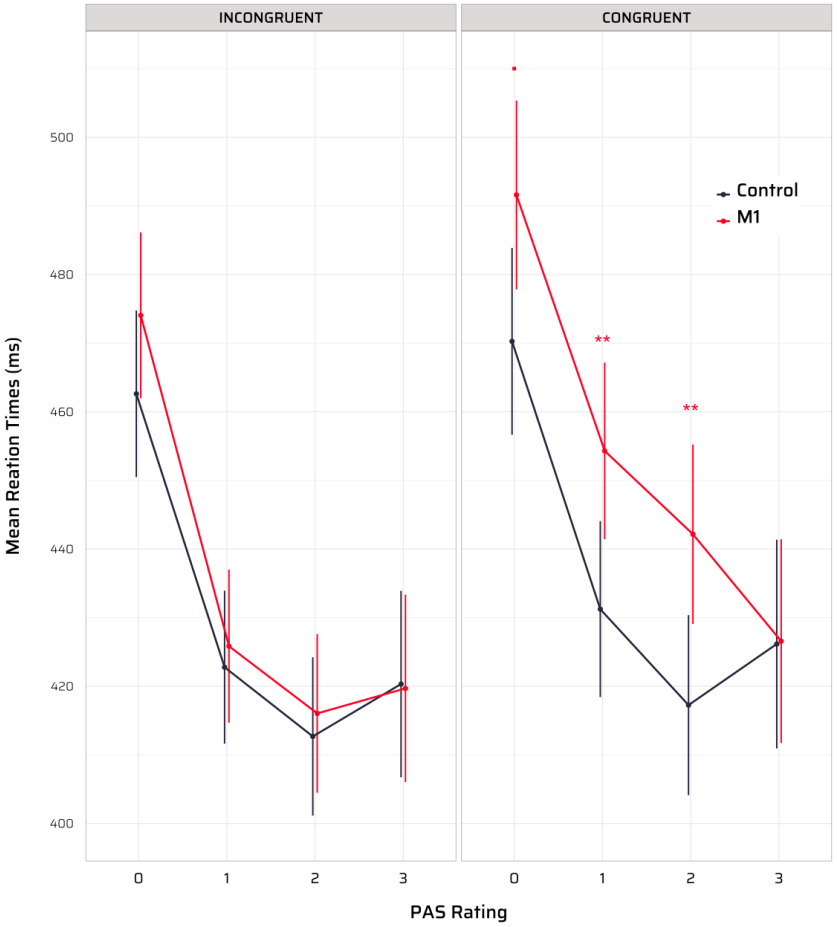

Fig. 5. Identification task RTs as a function of the stimulus congruence and the TMS condition. Error bars represent SEs.

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3.4 Metacognitive efficiency

We chose M-ratio as the measure of metacognitive efficiency. Calculating measures of metacognition based on Signal Detection Theory requires including button press counts for both options, therefore it is impossible to calculate them for response congruence. We fitted a linear mixed-effect model with condition as a fixed factor and subject-specific intercepts. Therefore, we tested only if there was a change in metacognitive efficiency between M1 and control conditions and did not find a significant effect ($t(45) = -0.30$, $p = .766$).

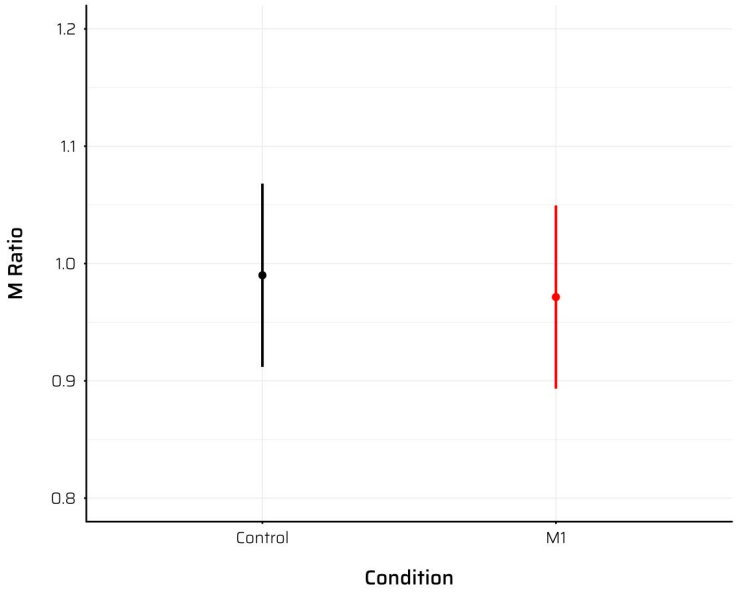

Fig. 6. M-ratio depending on condition. Error bars represent SEs.

3.5 MEP amplitudes

We fitted a linear mixed-effect model with condition and response congruence as fixed effects, random slopes for response congruence, and subject-specific intercepts. There was a significant increase in MEP amplitude in the M1 condition compared to the control condition ($t(6539) = 37.12$, $p < .001$). Additionally, there was a significant interaction between response congruence and condition ($t(3031.4) = 2.77$, $p = .006$). Pairwise comparisons revealed a significant increase in the amplitude in the M1 condition when stimulation was congruent with the performed response (z ratio = -4.13, $p < .001$). Additionally, we were interested if this increase is related to reported subjective experience, therefore we performed pairwise comparisons between congruent and incongruent trials within each PAS rating and condition combination. After correction, only comparisons for PAS ratings 2 and 3 in the M1 condition yielded significant differences (see Table 5 for detailed results).

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To check if it is possible to discern PAS rating from preceding MEP, we compared amplitudes from trials with different PAS ratings (see Table 6 for all estimates).

Table 5. Pairwise comparisons of regression coefficients between congruent and incongruent trials for every combination of condition and PAS rating. There was a significant difference between congruent and incongruent trials for PAS rating 2 and 3 within the M1 condition.

Congruent – Incongruent		**Estimate**	**Std. Error**	***z* ratio**	***p***
Control	PAS 0	-15.937	47.159	-0.3379	.8583
Control	PAS 1	52.082	33.526	1.5534	.2406
Control	PAS 2	1.831	35.700	0.0513	.9590
Control	PAS 3	16.671	52.544	0.3172	.8583
M1	PAS 0	-18.902	22.574	-0.8373	.6439
M1	PAS 1	-28.459	16.603	-1.7141	.2307
M1	PAS 2	**-57.256**	**18.879**	**-3.0326**	**.0097****
M1	PAS 3	**-104.464**	**29.559**	**-3.5340**	**.0033****

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Table 6. Pairwise comparisons between PAS ratings for congruent and incongruent trials within the M1 condition. Only trials with rating 3 were significantly different from others, irrespective of the congruence.

M1 condition		**Estimate**	**Std. Error**	***z* ratio**	***p***
Incongruent	0 - 1	31.28	18.28	1.7107	.3179
	0 - 2	45.47	20.22	2.2489	.1103
	0 - 3	-30.07	26.52	-1.1338	.6685
	1 - 2	14.20	16.62	0.8541	.8283
	1 - 3	**-61.35**	**24.05**	**-2.5511**	**.0524 ·**
	2 - 3	**-75.55**	**24.37**	**-3.1005**	**.0104 ***
Congruent	0 - 1	21.72	19.00	1.1431	.6627
	0 - 2	7.12	20.39	0.3492	.9853
	0 - 3	**-115.63**	**26.51**	**-4.3626**	**< .0001 *****
	1 - 2	-14.60	16.46	-0.8872	.8114
	1 - 3	**-137.35**	**23.68**	**-5.7993**	**< .0001 *****
	2 - 3	**-122.75**	**23.65**	**-5.1903**	**< .0001 *****

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

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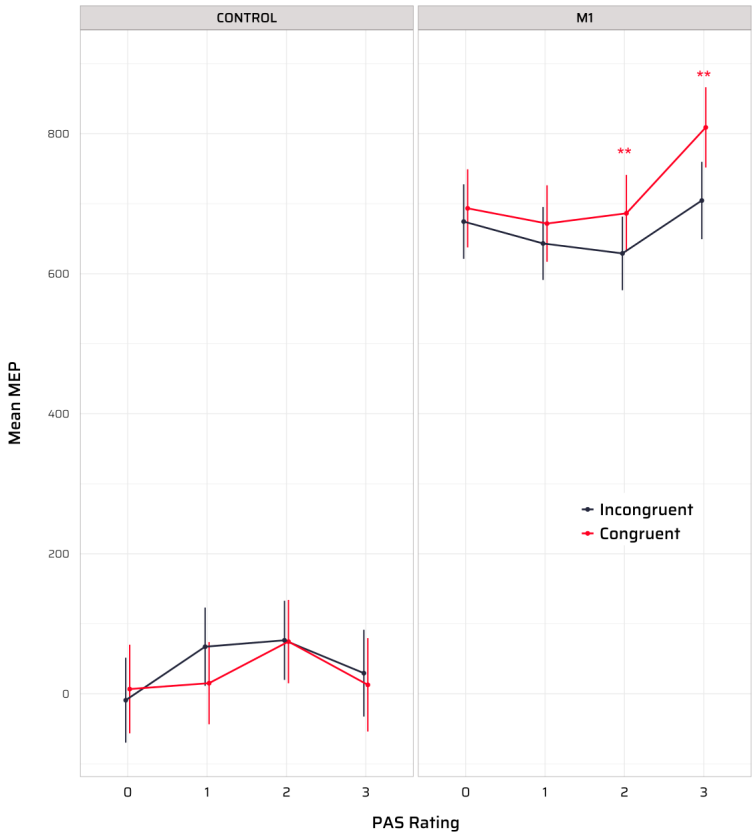

Fig. 7. Mean MEP amplitude for each PAS rating, lines represent response congruence, panels different conditions. Error bars represent SEs.

4. Discussion

In the present study, we aimed at gaining insight into non-perceptual influences on visual awareness. Through TMS-induced activity in the M1, delivered just after stimulus presentation but before behavioral response, we attempted to alter participants' experience of stimuli reflected in PAS ratings recorded at every trial. Our results show that sp-TMS stimulation did increase the reported visibility of stimuli without altering the objective performance of the participants. Additionally, we checked if this manipulation had any influence on a measure of metacognition, but no effect was found. Despite a procedure with fairly postponed behavioral reaction, we observed higher RTs in trials with sp-TMS to the M1, but only in those accompanied by low PAS ratings. Finally, MEP amplitudes calculated from EMG data in response to sp-TMS were indicative of subsequent PAS ratings, but only if participants declared high visibility.

Based on the presented data, we suggest that this externally induced activity in M1 served as additional information for evidence accumulation processes that lead to subjective ratings and behavioral responses. RT results seem to support this conclusion, reflecting the prolonged activity of processes integrating information from the motor system in response to additional neuronal activity,

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predominantly when the perceptual evidence was not fully decisive. Finally, this process of evidence accumulation seems also to be reflected in M1 excitability measured with MEPs. In our experiment, this relation was present only for trials with high PAS ratings which might be a consequence of (1) participants having already decided on their subsequent response, which in turn would trigger preparatory activation in the motor cortex, (2) participants having not decided but the information about the stimulus was passed from dorsal visual stream to M1.

4.1 Additional evidence-related increase in subjective ratings

Our primary goal was to verify to what extent the activity of the motor system alone can contribute to the processing of perceptual information. Additional engagement of motor activity, irrelevant to the performed task, has already been shown to influence awareness ratings in the work of Siedlecka, Hobot et al. (2019). However, their design did not allow for the exclusion of confounding factors, like the introduction of additional visual stimulation or differences in attentional engagement, because participants were explicitly instructed and cued to perform a second task. In this study, we expanded upon that paradigm with direct excitation of M1 that would allow us to reduce the influence of mentioned confounds. Nevertheless, our conclusions are similar and reinforce those of Siedlecka and colleagues, that additional activation in the motor system, even if unrelated to the main task, will be incorporated and interpreted as evidence by the decision processes.

Unlike them, we found only evidence for integration in response congruent trials, whereas their results showed an increase in subjective ratings irrespective of congruence. This could be a consequence of the sheer fact that in their study participants performed an additional reaction. The second task was very simple and instructions focused on the speed of reaction, therefore in each trial participants could prepare both reactions simultaneously, which would result in additional motor cortex activation in both hemispheres. In our study, the TMS-induced activation was weaker than that related to actual movement, which might explain why there was no effect observed in the incongruent trials. Our results provide further evidence that findings reported by Siedlecka, Hobot, et al. (2019) resulted from the motor activity and not from some perceptual or attentional processes.

A similar direct approach was undertaken by Fleming et al. (2015), where sp-TMS was used to stimulate M1 as well as the higher-level PMd. They also report an increase in subjective ratings in congruent trials, however, the effects were limited only to the stimulation of PMd and trials with correct responses. One explanation of differences concerning M1 stimulation could be the intensity of the pulses. Fleming and colleagues set their TMS intensity to 90% AMT, so below the threshold of overt motor activity, while in our study we delivered supra-threshold stimulation at 110% of individual RMT. Weaker stimulation might also account for not observing any effect on the error trials. It is also possible, that increased activation in different parts of the motor system serves different metacognitive purposes, resulting in the discrepancies between studies.

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Additional activation in M1 could be interpreted as a signal strengthening the already chosen outcome, building up confidence in response performed. In that sense it would be isolated from assessing actions in response incongruent trials, i.e. performed with non-stimulated hand. That is the case in our experiment, where the effect of stimulation is significant only with response congruence. On the other hand, activation in PMd would strengthen the motor plan related to congruent response, that in the decisional process preceding behavioural response would compete with the analogue plan in the other hemisphere, while influencing both primary cortices (Reis et al., 2008). Such influence should be observed in congruent and incongruent trials (although in opposite direction), as well as for correct and incorrect trials. Fleming et al. (2015) themselves notice possible opposite effects of their stimulation in the other condition but note that lack of power possibly not allowed for them to observe a significant difference. Therefore, this possibility is yet to be verified in an adequately powered follow-up study.

The hypothesis of different importance of PMd and M1 cortices for the metacognitive processes can be also interpreted from the analyses of metacognition measures. Fleming et al. (2015) reported lower metacognitive efficiency (measured with M-ratio) for incongruent compared to the congruent condition. This was true only for the PMd stimulation delivered before the response. They found no effect in the other conditions. It is difficult to interpret the lack of effect for M1 stimulation when no TMS influence was found significant. However, it is in agreement with our data, where we also did not find any effect on metacognitive efficiency between conditions. These results might further strengthen the suggestion that PMd activation is incorporated into the evaluation of action performance in light of perceptual evidence, decreasing M-ratio measure in the incongruent trials through additional activation of competing motor scheme that accounts as evidence against chosen response. On the other hand, additional M1 activation would increase evidence for the congruent response (correct or not), in consequence, keeping the metacognitive measure on the same level. Additionally, this effect would be isolated only to congruent trials, resulting in no overall change in metacognitive sensitivity while still impacting mean subjective ratings.

Another interesting difference between our results and those reported by Fleming et al. (2015) is related to RTs. In their study, only a general speeding effect of pre-response stimulation was found, with no specific effect for the congruent trials (although it seems the speeding effect of congruence might not be significant because of lack of statistical power, as authors suggest themselves). This seems in line with research showing increased excitability in M1 cortex in response to PMd stimulation (Koch et al., 2006), although this relation appears sensitive to the timing of the TMS pulses. Precisely, stimulation of left PMd is often reported as affecting both M1 cortices (Fujiyama et al., 2016), which could explain the general speeding effect. In comparison, our results show a clear congruence effect, increasing RTs for trials where participants declared lower visibility of stimulus. We interpret these results as a consequence of evidence accumulation processes as well, where for trials with high visibility, the decision process ends before stimulation, so no additional evidence is needed.

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When the stimuli are not as clear, these processes operate longer and on a lesser amount of evidence. This not only makes TMS-induced activity appears "on time" to be incorporated, but also additional information can be of higher importance since the perceptual evidence is scarcer. It might be the case, that this was possible partially thanks to moving objective response at the end of the trial, so the accumulation processes could last longer. Finally, here we also observed results suggesting M1 stimulation being an isolated intervention, affecting only congruent trials while having no effect on incongruent.

4.2 MEP as a measure of accumulated evidence

Our additional hypotheses concerned using MEP as an objective measure allowing to quantify the neuronal correlate of evidence accumulation. MEP is frequently used in literature as a read-out of the state of excitability of the stimulated motor cortex (Bestmann & Krakauer, 2015). In this approach M1 is treated as a recipient of some decision processes occurring outside of it, that exert influence through modulation of M1 excitability via direct or indirect connections to motor and premotor cortex (Klein-Flügge & Bestmann, 2012; Klein-Flügge et al., 2013). Crucially, there is evidence that cognitive manipulation can influence M1 excitability, be it spatial attention (Mars et al., 2007), values assigned to different responses (Klein-Flügge & Bestmann, 2012) or contextual uncertainty (Bestmann et al., 2008). What is important, these accounts also show the influence that is specific to an effector of interest, displaying no relation when e.g. stimuli presented to a participant are uninformative. However, when the connection with particular response is present, MEP was reported to scale along information, e.g. expected the outcome of that decision process (Klein-Flügge & Bestmann, 2012).

Our MEP results seem to agree with those findings. We found an effect of congruence in stimulation condition, where congruent trials were characterised by higher MEP amplitudes. This effect was observed predominantly in trials where participants reported high visibility of stimuli. Subsequent pairwise comparisons revealed that trials with the highest visibility had significantly higher amplitude than the trials with other ratings. This was true for congruent, but also for incongruent trials. These results seem to be complementary with the dynamics of evidence accumulation reflected in RTs. Taken together, they suggest that for highest visibility, where necessary evidence was already accumulated, the decision has been made before the stimulation occurred, giving time to increase the excitability in M1 in preparation for executing the response. On this stage, additional information from TMS does not play a crucial role. On the other hand, for trials with lower PAS ratings, accumulation of evidence is still ongoing, allowing TMS to play a noticeable role and increasing the mean PAS ratings and the RTs.

The significant difference between PAS rating 3 and others for incongruent trials is somewhat more complicated to interpret. Assuming that for best visible stimuli the evidence accumulation process finished earlier and transited into motor preparation phase, there are a couple of neuronal routes, that might be influencing M1. On one hand, it is known that left PMd is involved in motor preparation

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processes in both M1 cortices (Mars et al., 2007), that also might vary from excitatory to inhibitory influences, depending on different factors. Additionally, there is evidence that in preparatory period, there is an interaction between M1 cortices, that reflects non-task specific, global facilitatory processes. In such a case, even if participants were preparing movement in incongruent hand, it would increase excitability in congruent hand. Additionally, there is an observable increase in congruent MEPs and a decrease in incongruent MEPs, but it is usually observed much closer to actual manual response than the timing of our stimulation (Klein-Flügge & Bestmann, 2012). This makes it more probable that we captured the general preparatory mechanisms, that could nonetheless discriminate between high visibility and congruent responses. Results from Gajdos and colleagues (2019) could be interpreted in agreement with this hypothesis, as there was a significant effect of ipsilateral as well as contralateral subthreshold activation. Taken together, these results seem promising for using MEP to probe the evidence accumulation process in the cortex, but additional experiments, crucially with stimulation closer in time to response are necessary to confirm this claim.

4.3 Possible mechanisms of addition evidence integration

Our experiment provides new evidence for a distinct path in a complex system integrating information between perception and action. However, the structure of this system and the nature of interactions between its parts is still largely unknown. This leaves an open question on what is the neuronal mechanism that leads to the effects observed in this study.

There is a growing body of evidence showing that PFC, especially dlPFC, should be considered a key structure for integrating information necessary for metacognitive processes (Fleming & Dolan, 2012; Rounis et al., 2010), which are thought to be then reflected in subjective reports, like PAS or CS ratings (Lau & Rosenthal, 2011). Assuming the central role of dlPFC in the decision process taking place in our experiment, there are strong presumptions to treat sp-TMS manipulation effects in our study as an indirect influence since there are no direct connections between dlPFC and M1 cortex (Passingham, 1993). This would imply that the most probable route for the integration of information from M1 is through somatosensory cortex. There is ample evidence of the reciprocal connection between M1 and S1 cortices (Gandolla et al., 2014), through which TMS-induced activity would induce somatosensory cortex activity resembling feedback information about the movement of the finger used to press the response button.

Additionally, this information transfer between M1 and S1 could also happen through muscle activity. This could explain why our experiment, where we stimulated the participants' M1 above their RMT, and study by Siedlecka et al. (2019) in which participants performed an actual additional behavioural response, found a significant influence on visual awareness ratings. Both of the above explanations are consistent with results from Fleming et al. (2015) since their stimulation was below individual RMT, limiting the possibility of sufficient direct influence from M1 on S1 or sufficient muscle activity to

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trigger somatosensory feedback. Similarly, results provided by Gajdos et al. (2019) would suggest that trials labelled as containing a significant partial pre-response muscle activation would also alter somatosensory readout that would be later integrated into the decision process about the stimulus itself.

Finally, the design of the procedure, with reversed order of objective and subjective response and a significant delay between stimulus presentation, sp-TMS delivery, and objective response allowed us to observe the effects of evidence accumulation processes in part independently from the decision process itself. We think that these processes are reflected in effects reported for MEP analyses since the stimulation and actual behavioural response were separated by several seconds, much before motor preparation for the voluntary action should occur. Therefore, changes in MEP amplitude seem to reflect the accumulation of perceptual evidence triggered by the presentation of the stimulus. This seems possible based on various connections to the M1, especially from the PPC.

There is a substantive body of knowledge about neuronal pathways integrating perceptual information and action, most explicitly described in the works of Goodale and Miller as “perception for action” in the dorsal stream (1992). PPC is thought of as a central perceptual hub for controlling and guiding behaviour. Its influence was considered to be predominantly indirect, through vast connections with higher motor areas (Kaas & Stepniewska, 2016). PPC functions as a multisensory integration area (Koch et al., 2007) that plays an important role in performing skilled voluntary movements, especially if they require visual input (Vingerhoets, 2014). In recent years there is growing evidence that PPC has also direct connections to M1 (Isayama et al., 2019; Schulz et al., 2015). These connections could serve as a potential pathway for perceptual evidence accumulated in PPC to directly influence M1 excitability in situations, where motor plans are simple or well-trained (as in our experiment). This could explain differences in excitability of M1 observed in our experiment in trials with high PAS ratings as there would be more information transferred from PPC to M1. Additionally, the PPC could facilitate execution of response related to the accumulated evidence, which would explain the differences in the MEP amplitudes between congruent and incongruent trials.

On the other hand, PPC would likely also be involved in integrating mentioned somatosensory feedback information to evidence from other modalities, making it available for frontal areas responsible for decision making, action selection and execution. In normal circumstances, information from this sensorimotor feedback loop would be used to compare executed behaviour with the one planned in the frontal areas (e.g. dlPFC and PM). The more pronounced would be a mismatch, the lower would be the confidence in the correctness of one’s action. This might be the reason why the procedural manipulation of Fleming et al. (2015) resulted in a difference in metacognitive efficiency, where participants underestimated their performance in incongruent trials. Their stimulation of PMd altered the execution of response, creating a mismatch that would be caught by error monitoring processes.

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On the other hand, stimulation in our experiment was delivered early enough before the actual reaction, that this additional information could have been integrated before a motor plan was fully formed. This would increase selectively the evidence for stimulus associated with this particular effector, allowing participants to give higher subjective ratings for congruent trials. Results of RT analyses also indirectly indicate that this additional information influenced the decision process. Crucially, early integration of this motor information would not create a mismatch between planned and performed response, explaining why we did not observe any change in metacognitive efficiency.

Overall, our results shed new light on the relation between perceptual awareness and action by highlighting a novel pathway through which information from the motor system can be incorporated into perceptual and metacognitive processes. Combined with previous results, these findings broaden our understanding of interactions between action and perception, that allows humans to dynamically adjust and re-evaluate their interactions with the environment. Significance of influence of non-perceptual information calls also for reconsideration on theories of perceptual awareness that are primarily focusing on processing sensory input.

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