Alpha stimulation of the human parietal cortex attunes tactile perception to external space

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Short Title:

Frequency-coded spatial representation in the PPC.

Keywords: human perception, touch, tactile remapping, alpha rhythm, Intra-Parietal Sulcus (IPS), transcranial magnetic stimulation (TMS), entrainment.
**Highlights**

*These are a short collection of bullet points that convey the core findings of the article. This list of points will be displayed online with the summary of the article but will not appear in print. Highlights are required for papers published from January 2010 onward and should be included in the main text. Specifications: up to 4 bullet points can be included; the length of an individual bullet point should not exceed 85 characters (including spaces); only the core results of the paper should be covered.*

- We found a causal link between 10Hz TMS and tactile detection in humans
- Pre-stimulus 10Hz TMS at IPS leads to contra vs. ipsi-lateral detection improvement
- This effect expresses in an external reference frame independent of posture
- This effect of TMS on perception is specific for frequency and site of stimulation
In Brief

The "In Brief" is a short summary of the main take-home message of the paper that appears when a reader hovers over "In Brief" in our online Table of Contents (effective from Jan 2014). Please could you provide a suggested In Brief summary in the "Author Comments" field when you upload your finalised files: the summary should be a maximum of 315 characters including spaces, or a maximum of 50 words, and should be written in the present tense, referring to the authorship as "Firstauthor" (papers with one author), "Firstauthor and Secondauthor" (papers with two authors), or "Firstauthor et al." (papers with 3+ authors).

The results establish a tight causal link between a concrete form of brain activity (10 Hz oscillation) and a specific type of spatial representation (external reference frame). This finding reveals a fundamental property of how the parietal cortex encodes information in the human brain.
Summary

An intriguing question in neuroscience concerns how somatosensory events on the skin are represented in the human brain. Since Head and Holmes’[1] neuropsychological dissociation between localizing touch on the skin and localizing body parts in external space, touch is considered to operate in a variety of spatial reference frames [2]. At least two representations of space are in competition during orienting to touch: a somatotopic one, reflecting the organization of the somatosensory cortex (S1)[3] and a more abstract, external reference frame that factors postural changes in relation to body parts and/or external space [4, 5]. Previous TMS studies suggest that the posterior parietal cortex (PPC) plays a key role in supporting representations as well as orienting attention in an external reference frame [4, 6]. Here, we capitalized on the transcranial magnetic stimulation (TMS) entrainment approach [7, 8], targeting the intra parietal sulcus. We found that frequency-specific (10 Hz) tuning of the PPC induced spatially-specific enhancement of tactile detection that expressed in an external reference frame. This finding establishes a tight causal link between a concrete form of brain activity (10 Hz oscillation) and a specific type of spatial representation, revealing a fundamental property of how the parietal cortex encodes information.
Results and Discussion

According to human electrophysiology and magnetoencephalography, inter-hemispheric imbalance in alpha (8-12 Hz) neural activity at the PPC characterizes brain states related to shifting spatial attention in different sensory modalities [9-11]. Yet, the correlational nature of these findings is inconclusive regarding the causal role of the oscillatory alpha pattern. Recent visual studies have used rhythmic TMS at the PPC to entrain neural activity in the alpha range [12] that leads to increased sensitivity in the ipsilateral hemifield and, to lowered sensitivity in the contralateral one (compared to other stimulation frequencies like theta, 5 Hz, or beta, 20 Hz) [8]. Here we use this innovative approach in the modality of touch to go beyond previous demonstrations that TMS at the PPC disrupts tactile remapping [4, 6], and to address whether entraining neural activity with TMS enables tactile orienting. The question is whether inducing 10 Hz rhythmic activity in the PPC causes spatially-specific modulation in tactile detection and, most importantly, in which reference frame it does so.

In Experiment 1, participants (n=12) performed a signal detection task on vibrotactile stimuli presented to the right or left index finger unpredictably. In the pre-stimulus interval we applied rhythmic TMS pulses at 10 or 20 Hz over the intra-parietal sulcus (IPS), in the PPC, or over the primary somatosensory cortex (S1), so that the last pulse of TMS was synchronized with the onset of the tactile event (Fig. 1a). TMS effects were assessed relative to sham stimulation at equivalent frequencies, with the coil held perpendicular to the scalp. TMS at 10 Hz over the IPS modulated target detection in a spatially and frequency specific manner, as revealed by the triple interaction between TMS area (IPS, S1), TMS frequency (10 Hz, 20 Hz) and tactile side (contralateral, ipsilateral
hand) \(F_{(1,10)}=7.64, p=0.02\); ipsilateral enhancement over contralateral at 10 Hz in the IPS, \(t_{(10)}=-5.64, p=0.0002\]. That is, TMS at 10 Hz over IPS impaired tactile detection for contralateral stimuli [t-test against baseline, \(t_{(11)}=-3.59; p=0.004\], and improved detection of stimuli at the hand ipsilateral \([t_{(11)}=3.49; p=0.005]\) to the hemisphere of TMS application (Fig. 1b). Instead, 20 Hz stimulation at the IPS was ineffective. The stimulation of S1 led to spatially specific modulation but, in contrast to IPS, not in a frequency-specific fashion, since both 10 Hz \([t_{(11)}=-2.93; p=0.01]\) and 20 Hz \([t_{(11)}=-3.33; p=0.007]\) TMS worsened sensitivity to contralateral stimuli (Fig. 1c). This result is consistent with previous correlational evidence claiming that both alpha and beta (13–30 Hz) rhythms in S1 are associated to tactile expectation [13], though they could also reflect the lack of frequency specificity of pre-stimulus TMS effects in S1. Importantly, the results of IPS stimulation provide clear evidence for a specific role of 10 Hz rhythmic activity at the PPC in tactile spatial perception. Together with previous findings in vision [8] this suggests that 10 Hz in the IPS might tune perception at a supra-modal level [14], mimicking the effects of spatial attention deployment.

The finding of Experiment 1 offers the opportunity to uncover which kind of spatial representation is driven by 10 Hz stimulation at the IPS. To this aim, in Experiment 2 we tested the spatial frame of reference in which target detection effects express across postural changes. We applied pre-stimulus 10 Hz TMS to the IPS as participants \(n=12\) adopted an uncrossed (as in Experiment 1) or crossed hand posture (see Fig. 2). Crossing hands about the body midline misaligns somatotopic vs. external reference frames, as the hand anatomically contralateral to the hemisphere of TMS application is now placed in the ipsilateral side of external space. Thus, the question is whether alpha rhythm in the IPS will
improve target detection in terms of somatotopic space, that is, at the anatomi
cally ipsilateral hand, or else, in an external frame of reference (shared with vision), that is, at the anatomi
cally contralateral hand, now placed in the ipsilateral hemispace. We used an arrhythmic TMS (arTMS) baseline condition, instead of sham, to further control for generic TMS effects and secure a frequency-specific interpretation [12]. Whereas the uncrossed hands results replicated the advantage in tactile detection for the ipsilateral over the contralateral hand \([t_{(10)}=-3.19, p=0.01]\) at 10 Hz TMS (Fig. 2a), when participants held their hands crossed, the effects of 10 Hz TMS reversed, revealing a clear organization based on an external frame of reference [Fig. 2b; contralateral vs. ipsilateral \(t_{(10)}=2.34, p=0.04\)]. That is, when the anatomically contralateral hand was crossed over the ipsilateral side of space, detection of tactile events was better, rather than worse [crossed position, \(t_{(11)}=2.29; p=0.04\)], compared to the anatomically ipsilateral hand. Thus, remarkably, just by crossing the left hand over the right hemispace (or \textit{vice versa}) inverts the effects of TMS on sensory detection, as revealed by the significant interaction between posture and target side \([F_{(1,10)}=11.39; p=0.007]\). Summarizing, the entrainment of alpha activity in the ipsilateral hemisphere favoured tactile perception whereas entraining alpha rhythm in the contralateral hemisphere interfered (see Fig. 1b and 2a). The pattern of spatial effects observed in Experiment 2 clearly conforms to an external frame of reference, rather than to the anatomi
cally-based organization typical of the somatosensory cortex (see Fig. 2b).

We further addressed the role of alpha (Experiment 3, \(n=12\)) and beta (Experiment 4, \(n=6\)) rhythmic stimulation in S1 using an arrhythmic TMS baseline and manipulating posture (crossed vs. uncrossed). Gauging the effects of pre-stimulus 10 Hz and 20 Hz TMS at S1 under crossed and uncrossed hands posture should offer a comparison for the spatially
and frequency specific pre-stimulus TMS effects over IPS found in Experiments 1 and 2. Here, the interaction between posture (crossed vs. uncrossed) and target side (contralateral vs. ipsilateral) failed to reach significance [Experiment 3: $F_{(1,10)}=1.24; p=0.3$; Experiment 4: $F_{(1,4)}=0.23; p=0.66$]. Tactile sensitivity was not biased by pre-stimulus rhythmic TMS at 10 or 20 Hz in S1, as compared to the arrhythmic TMS baseline (see Supplemental Table S3 and S4 and Supplemental Experimental Procedure). The outcome of S1 stimulation contrasts with the role of specific 10 Hz oscillatory activity in the PPC, where pre-stimulus 10 Hz stimulation in IPS effectively led to a shift in detection performance, and coded for an external spatial frame of reference. Note that the lack of a contralateral performance decrement of rTMS to S1 in Experiments 3 and 4 (see Supplemental Experimental Procedure for further evidence) can be explained by the use of an arrhythmic TMS baseline, instead of sham. Therefore, this result does not mean that TMS in S1 fails to affect performance, but just that it failed to do so in a frequency-specific way.

In conclusion, the present finding may complement prior claims about where [4, 6] and when [5, 15] the remapping of tactile space takes place in the human brain, shedding new light on how spatial representations are encoded by PPC neural activity. At present, it is difficult to resolve whether 10 Hz PPC activity leads to remapping itself, supports the orienting of attention toward an already remapped representation of tactile space or, even whether attention and remapping are two sides of the same coin [15]. In any case, our results provide strong causal evidence for the functional role of alpha oscillatory activity in the PPC as a form of coding spatial representations in an abstract, external format beyond sensory specific (somatotopic) organization. Indeed, externally-induced alpha modulations
of these representations had a measurable behavioural consequence. This alpha oscillation in the human IPS might be a candidate pattern to orchestrate the alignment of tactile representations (or tactile attention) with other sensory modalities under a common coordinate system. In addition, we note that the present finding might help provide the physiological grounds for the unexpected alleviation of tactile extinction in brain-damaged patients as they cross their contralesional (affected) hand over the ipsilateral space[16], paving the way for further understanding of this clinical condition. Based on the present results, we suggest that alpha spatio-temporal regime in the IPS is causal for sampling tactile sensory information from the external world, supporting a common spatial register for the representation of spatial information.
Acknowledgements:

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Competing financial interests:

The authors declare no competing financial interests.
Figure Legends

Figure 1. (a) Schematic representation of a trial. Participants fixated on a central LED that flickered (60 ms) at the onset of each trial. The TMS pulse train was delivered after a variable delay. The vibrotactile target was presented at the right or left index finger pad (unpredictably), synchronized with the last TMS pulse. The participants were asked to perform a signal detection task (signal vs. noise) by giving (unspeeded) responses via a foot pedal. (b) and (c) represent detection performance \([\Delta d' = d'(\text{TMS})-d'(\text{sham})]\) in Experiment 1 for IPS and S1 stimulation conditions (respectively) for the hand anatomically contralateral (dark gray) and ipsilateral (light gray) to the hemisphere of TMS. The ANOVA on detection performance included the within-participant factors stimulation area (IPS, S1), stimulation frequency (10 Hz, 20 Hz) and target side (contralateral, ipsilateral to TMS) and the between subjects factor TMS hemisphere of stimulation (left vs. right). The asterisks indicate significant differences (p<0.05; see text for details). The main effect of TMS hemisphere (left vs. right) or any other interaction involving this factor were not significant. Response criterion was also analyzed and was not affected by the experimental manipulations. Data for all conditions are available in Supplemental Table S1.

Figure 2. Detection performance \([\Delta d' = d'(\text{TMS})-d'(\text{arTMS})]\) in Experiment 2 in the uncrossed (a) and crossed (b) hand postures, for anatomically contralateral (dark gray) and ipsilateral (light gray) hands. The ANOVA on detection performance included posture (uncrossed/crossed) and target side (contralateral, ipsilateral to TMS) as within subject factors and the between subjects factor hemisphere of TMS (left vs. right). Asterisks indicate significant differences (p<0.05; see text for details). The main effect of TMS
hemisphere (left vs. right) was not significant and did not interact with posture. The response criterion (c) was not affected by the experimental manipulations. Data for all conditions are available in Supplemental Table S2.
Experimental Procedures

Participants

Forty-two healthy volunteers with normal or corrected to normal vision and no contraindications for TMS [17] participated in four experiments; in particular Experiment 1 (n=12; 6 women; age range 19–36 years); Experiment 2 (n=12; 7 women; age range 19–30 years); Experiment 3 (n=12; 6 women; age range 19–29 years); Experiment 4 (n=6; 3 women; age range 19–29 years). All gave written informed consent to participate in the study, in accord to the Declaration of Helsinki and approved by the ethics committee CEIC Parc de Mar (University Pompeu Fabra, Barcelona, Spain).

Experiment 1

Vibrotactile stimuli and task

Vibrotactile stimuli were delivered by Oticon-A bone conduction vibrators (3.8 cm² vibrating surface; Oticon) attached on the index finger pad of the left and right hand. The detection task involved a two-alternative forced choice between target and no-target events (equiprobable). The target signal was a 50ms 200 Hz sine wave (10 ms ramps), followed by a white noise mask of 150 ms, whereas no target trials were 200 ms of white noise. The intensity of the target signal was adjusted to a d’≈1 threshold for each participant and each hand using an adaptive procedure [18] prior to each experimental session. The participants’ hands rested palm-down inside a black box bearing the fixation LED at the centre of its top surface. The hands were placed equidistant to the fixation LED and out of the participant’s sight. We encouraged the participants to relax their fingers and wrist as much as possible during the trials, and to move their arm in between the blocks in order to
avoid numbness sensation. Participants provided the responses (target / no-target) by releasing one of the two foot pedals (toe or heel) according to the instruction (response mapping counterbalanced). The response foot was chosen to be homologous to the side of TMS stimulation, in order to avoid possible contamination in the response execution. Immediately after the response, feedback was provided, in order to maintain the response criterion as stable as possible. The next trial started after 6 s.

**TMS protocol**

TMS was applied with a Magstim Rapid² transcranial magnetic stimulator via a 70 mm figure-of-eight coil (Magstim) over the left or right hemisphere, at the posterior parietal cortex (IPS) or the somatosensory cortex (S1). The positioning of the coil was monitored throughout the session using a SofTaxic navigator system (E.M.S.) based on individual MRIs. For IPS localization we used Talairach coordinates [right parietal: 17, -65, 54; left parietal: -19, -63, 60] [8, 19] and for S1 we used anatomical landmarks. The coordinates chosen for IPS localization have been previously used effectively for entraining visual orienting with TMS [8], but are slightly superior compared to previous studies on tactile remapping [see [4, 6]. We applied five pulses of TMS at 10 Hz or 20 Hz over the target areas (IPS and S1), with the coil held tangential to the scalp. In all conditions TMS was delivered before the presentation of the vibrotactile stimulus [8, 12], so that the last pulse was synchronized with the tactile stimulus presentation (see Figure 1a). During sham control conditions the coil was oriented perpendicular to the scalp over a point in between IPS and S1, at 10 Hz or 20 Hz depending on the condition. All the participants ran two experimental sessions on two consecutive days, each including the stimulation of one target area at both frequencies and one sham session. Half of the participants were stimulated on
the right hemisphere and the remaining on the left hemisphere (counterbalanced across participants). TMS intensity was adjusted at 100% of visible motor threshold [20] at the beginning of each experimental session (average intensity was 53% ± 5% and 53% ± 3%, for sessions 1 and 2, respectively).

Procedure

After initial familiarization and training (20 trials), the threshold for the vibrotactile stimulation intensity was assessed for each participant [18]. The experiment consisted of two blocks of 40 trials for IPS and S1 TMS application (for a total of 80 trials for each area) at each stimulation frequency. In the sham condition, we collected data from one session (40 trials) for each stimulation frequency. The order of the target areas (IPS, S1 and sham) and of the frequencies of the stimulation (10 and 20 Hz) was randomized for each participant and session.

Experiments 2-4

The vibrotactile stimuli, the task and the TMS protocol were like that of Experiment 1 except that the control condition consisted of effective but arrhythmic stimulation (arTMS). Five pulses of TMS were discharged at random times within the same temporal window as in the rhythmic 10 Hz TMS condition, only that the last TMS pulse was synchronized with the tactile stimulus (like in the rhythmic TMS trials). In this way any unspecific effect associated to TMS, like TMS discomfort, somatic-sensations, sound, and monitoring were the same in the arTMS and the rhythmic TMS conditions [see 12]. In Experiment 2 participants were stimulated over the IPS only, at 10 Hz and arrhythmically (two 40 trial blocks for each TMS condition). Participants ran these conditions twice, once with their
hands uncrossed and once in crossed hands posture. The order of the TMS (10 Hz IPS, arTMS) and body posture (uncrossed, crossed) was randomized across participants. The average stimulation intensity was 51% ± 4 of maximum stimulator output.

In Experiment 3 the target TMS area was the S1. The average stimulation intensity was 50% ± 4 of maximum stimulator output. In Experiment 4, rhythmic TMS was applied at 20 Hz over the S1. The average stimulation intensity was 49% ± 5 of maximum stimulator output (see Supplemental Experimental Procedure for further details).
References:


a. Trial example

Fix
TMS
Target
2AFC
Response
ITI

60 ms 500-1,000 ms
10 Hz, 400 ms
200 ms
100-200 ms
Max 2,000 ms
6,000 ms

b. Intra-Parietal Sulcus
c. Primary Somatosensory Cortex

\[ \Delta \delta = \delta(TMS) - \delta( Sham) \]

10 Hz 20 Hz 10 Hz 20 Hz

Contralateral hand touch
Ipsilateral hand touch

n=12
Intra-Parietal Sulcus
TMS @ 10Hz

Uncrossed  Crossed

- Controlateral hand touch
- Ipsilateral hand touch

n=12
Inventory of Supplement information

Supplemental Data:
- Table S1-Related to data presented in Figure 1
- Table S2-Related to data presented in Figure 2
- Table S3-Related to Experimental Procedure (Experiment 3)
- Table S4-Related to Experimental Procedure (Experiment 4)

Supplemental Experimental Procedures:
Description of the participants and further data analysis related to Experiment 3 and 4.

Supplemental References
Supplemental Data

<table>
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<th>20 Hz TMS</th>
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<td>sham</td>
<td>IPS</td>
<td>S1</td>
<td>sham</td>
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<td></td>
<td>contra</td>
<td>ipsi</td>
<td>contra</td>
<td>ipsi</td>
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<tr>
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<td>1.47 (0.28)</td>
<td>1.28 (0.52)</td>
<td>1.07 (0.49)</td>
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<td>Mean c (s.d.)</td>
<td>-0.19 (0.52)</td>
<td>0.03 (0.49)</td>
<td>-0.23 (0.55)</td>
<td>-0.26 (0.38)</td>
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Table S1. Inter-participants mean signal detection data (d’ and c) in Experiment 1, (N=12).

<table>
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<tr>
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<td></td>
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<td>ipsi</td>
<td>contra</td>
<td>ipsi</td>
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<tr>
<td>Mean d' (s.d.)</td>
<td>1.36 (0.85)</td>
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<td>1.41 (0.89)</td>
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<td>Mean c (s.d.)</td>
<td>0.23 (0.53)</td>
<td>0.16 (0.46)</td>
<td>0.13 (0.58)</td>
<td>0.35 (0.46)</td>
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Table S2. Inter-participants mean signal detection data (d’ and c) in Experiment 2, (N=12).
Please note that the labels contra and ipsi always refer to the anatomical hand with respect to the hemisphere of TMS application (see also Figure 2).
Table S3. Inter-participants mean signal detection data (d’ and c) in Experiment 3, (N=12). Please note that the labels contra and ipsi always refer to the anatomical hand with respect to the hemisphere of TMS application. The ANOVA on detection performance [Δd’= d’(TMS)-d’(sham)] included the within-participant factors posture (crossed, uncrossed) and target side (contralateral, ipsilateral to TMS) and the between subjects factor TMS hemisphere of stimulation (left vs. right). Neither main effects [posture: F(1,10)=0.05; p=0.82; target side: F(1,10)=2.19; p=0.17] nor interaction effects [F(1,10)=1.24; p=0.3] were observed.

Rhythmic 10Hz TMS on S1 appeared to only marginally affect sensitivity for the contralateral target side in the uncrossed hand position [uncrossed hands contralateral touch t-test against baseline t(11)=−1.84; p=0.09; uncrossed hands ipsilateral touch t-test against baseline, t(11)=1.45, p=0.18; crossed hands contralateral touch t-test against baseline, t(11)=0.08, p=0.94; crossed hands ipsilateral touch t-test against baseline t(11)=0.27, p=0.79]. Contrary to the rest of the experiments, we observed an interaction between posture and target side [F(1,10)=8.14; p=0.02] in the response criterion (c), due to a significant reduction in criterion specific for the 10Hz crossed-hands condition [t-test against baseline t(11)=−2.43, p=0.03]. Though other studies have reported response criterion shifts related to TMS stimulation in other brain areas [S1], the origin and signification of the present criterion shift is unclear, and definitely tangential to the main result of this study in terms of sensitivity.
<table>
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<tr>
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<td>20Hz S1 contra</td>
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<tr>
<td></td>
<td>ipsi</td>
<td>ipsi</td>
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<tr>
<td>Mean d’ (s.d.)</td>
<td>1.13 (0.94)</td>
<td>1.11 (0.97)</td>
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<td>1.44 (0.77)</td>
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<td>Mean c (s.d.)</td>
<td>0.06 (0.30)</td>
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<td></td>
<td>0.36 (0.30)</td>
<td>0.04 (0.69)</td>
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**Table S4.** Inter-participant mean signal detection data (d’ and c) in Experiment 4, (N=6).

The labels *contra* and *ipsi* always refer to the anatomical hand with respect to the hemisphere of TMS application. The ANOVA on detection performance [Δd’= d’(TMS)-d’(sham)] included the within-participant factors arm posture (crossed, uncrossed) and target side (contralateral, ipsilateral to TMS) and the between subjects factor TMS hemisphere of stimulation (left vs. right). Neither main effects [posture: F(1,4)=0.18; p=0.69; target side: F(1,4)=0.001; p=0.98] nor interaction effects [F(1,4)=0.22; p=0.65] were observed.

Rhythmic 20Hz TMS on S1 does not affect tactile sensitivity [uncrossed hands contralateral touch t-test against baseline t(4)=-0.04, p=0.99; uncrossed hands ipsilateral touch t-test against baseline t(4)=0.29, p=0.78; crossed hands contralateral touch t-test against baseline t(4)=-0.21, p=0.84; crossed hands ipsilateral touch t-test against baseline t(4)=-0.53, p=0.62].
Supplemental Experimental Procedures

Experiment 3 and 4

Data analyses (ANOVAs) on detection performance in Experiment 3 (n=12) and 4 (n=6), involving posture (crossed vs. uncrossed) and target side (contralateral vs. ipsilateral) as within subject factors and TMS hemisphere of stimulation (left vs. right) as between subjects factor are reported in the main text (see Results and Discussion) and in the Supplemental Tables S3 and S4.

To further address the functional relevance of pre-stimulus alpha and beta activity in S1, we tested twelve additional participants (6 women; age range 19–36 years) in the uncrossed condition only. The procedure, the stimuli and the task were exactly the same as described in the Experimental Procedure (Experiment 2-4), but TMS was applied at 10 and 20 Hz and arrhythmically (80 trials each condition).

Data from the uncrossed hand condition only from Experiments 3 (n=24) and 4 (n=18) were analyzed by two separated ANOVAs on the detection performance [$\Delta d’ = d’(TMS) - d’(sham)$] including the within-participant factor target side (contralateral, ipsilateral to TMS) and the between subjects factors TMS hemisphere of stimulation (left vs. right) and Experiment (3 or 4 vs. addendum). No significant effects were highlighted. Alpha frequency TMS on S1 did not affect detection performance neither for the contralateral target side [t-test against baseline, $t_{(23)}=0.15; p=0.88$] nor for the ipsilateral target side [t-test against baseline, $t_{(23)}=-1.35; p=0.19$]. Similar case was for 20 Hz TMS (contralateral target side, t-test against baseline, $t_{(17)}=-0.95; p=0.36$; ipsilateral target side, t-test against baseline, $t_{(17)}=-0.8; p=0.44$]. These results confirm that, in contrast to 10 Hz TMS at IPS,
tactile sensitivity is not biased by pre-stimulus rhythmic TMS at 10 or 20 Hz in S1.
Supplemental References