nature portfolio

Peer Review File

Probabilistic inference of social presence]{Probabilistic inference of social presence across brain scales reveals enhanced synaptic efficacy

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This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
This manuscript attempts to explore the neural underpinnings of social facilitation in monkeys and humans. I find the manuscript interest, with the potential to make a contirbution to the literature. However, there are a number of limitations primarily with the theoretical motivation, research design, and statistical analysis that prevent me from recommending this version for publication. I discuss these below.

-There seems to be a conflation between detecting whether a conspecific is present (social presence) and having a conspecific present that affects performance on a task (social faiclitation/inhibition). These are not the same thing, but are treated as such in the introduction. The authors should clearly speparate the perceptual mechanism from an attentional effect on behaviour. My belief is that they are more interested in the latter, but frame the paper as exploring the former. This needs to be clarified.
-Why are hidden causal mechanisms at the synaptic level necessary to explain social facilitation effects? There is an implicit assumption that this is the right level of analysis without any evidence support such an assumption. Please provide it.
-The paragraph structure of the introduction makes it difficult to follow the argument. Single paragraphs are packed with numerous points on varied topics. I suggest a revision to the structure where one self-contained ideas is present in one paragraph.
-The monkey data comes from a single monkey. I find this problematic for generalizability.
-The motivation for focussing just on executive control brain regions ACC and DLPFC in the monkey study is not clear to me. Why not sample neurons form across the social cognition brain network, including temporal lobe, prefrontal cortex, and precuneus?
-In social facilitation studies, the conspecific is often engaged in the task as well rather than being a mere observer. Would the pattern of results change if the actor believed that they could socially offload (see Tufft & Richardson, 2020) onto the conspecific because they are also engaged in the task?
-I understand the desire to focus on attention, but why restrict the EEG analysis just to the alpha band? There is potentially interesting results in the other bandwidths that were filtered out.
-There seems to be a facilitation effect for female humans only. Why might this be?

Reviewer #2

(Remarks to the Author)

This paper investigates how the mere presence of another individual alters attention-related neural dynamics and improves task performance. Drawing from experiments in both non-human primates and human participants, the authors propose that "social facilitation" arises partly through enhanced excitatory synaptic efficacy. They combine behavioral testing (an association-learning task in monkeys and a visuomotor interception task in humans) with advanced computational modeling at three levels of brain organization: (a) single neurons (micro), (b) cortical columns (meso), and (c) large-scale neural networks (macro). Their central finding is that social presence can strengthen connectivity in attention-oriented circuits across these scales, particularly by boosting recurrent excitatory connections, ultimately correlating with improved behavioral performance for certain groups (notably female participants in the human study).

This paper bridges single-cell recordings, local field potentials, and whole-brain EEG networks, offering a comprehensive account of how social presence might act at different levels of neural organization. The authors use well-controlled experimental designs in both monkeys (isolating mere presence vs. absence) and humans (observer vs. no-observer conditions). Here are some aspects of the paper that when addressed could improve the paper:

MAJOR:
1. Limited Neural Sampling in Monkeys: While the monkey data offer valuable micro- and mesoscale perspectives, effectively only one monkey's neural recordings were analyzed in detail (the second had data-quality issues). Such an N=1 for electrophysiological results raises concerns about individual variability. Only dlPFC and ACC were studied in-depth; no data exist for other areas that might also be sensitive to social presence (e.g., sensory cortices or subcortical arousal systems).

2. Differences Between Monkey and Human Tasks: The monkey association-learning task and the human interception task differ significantly in cognitive demands, which could limit cross-species comparisons. Although both tap into attentional processes, the tasks engage distinct motor and cognitive routines.

3. Sample Characteristics and Generalizability: In humans, the authors tested 27 participants split by sex. While they uncovered an intriguing sex difference, women showing clear facilitation, men not, the modest sample size calls for caution. Null results in the male group could reflect insufficient power or unexamined psychosocial factors (e.g., stress responses).

4. Stability of Parameter Estimates: Although the authors use advanced Bayesian inference techniques, they do not thoroughly address how the inferred parameters (e.g., synaptic gains at each scale) are under slight variations in the dataset or modeling choices. Such an analysis would increase confidence that small changes in sampling or data quality do not substantially alter their inferences.

5. Interpretation of Sex Differences: The study highlights that female participants showed increased effective connectivity in attention networks under observation, whereas males did not. Possible explanations (e.g., motivational or arousal differences) receive only brief mention, and deeper exploration of relevant literature (e.g., gender differences in stress or social facilitation) would help clarify why these effects emerged.

MINOR
Some methodological details (such as EEG source localization or the rationale for kinematic measures) appear mid-results rather than in a separate Methods section, occasionally disrupting the narrative flow.

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
All of my concerns were satisfactorily addressed. I am happy to recommend this version of the manuscript for publication.

Reviewer #2

(Remarks to the Author)
The authors have addressed all my concerns. Collectively, the revisions broaden support for the conclusions of the study and improve methodological interpretability, while addressing limitations and expanding on future directions.

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Response to Reviewers Manuscript, COMMSBIO-25-0266-T

“Probing other’s Presence: Probabilistic Inference Across Brain Scales Reveals Enhanced Excitatory Synaptic Efficacy”

Submission date: 25/01/2025
Revision date: 28/07/ 2025

We appreciate the time you and the reviewers have spent on this manuscript, as well as your insightful and constructive comments to improve the paper. We have now addressed the reviewers’ comments in our revised manuscript and provide here below detailed explanations of the changes. The changes in the manuscript have been marked in red color.

We have significantly revised both the introduction and discussion sections. Importantly, we have added the analysis for the second monkey to address the concern regarding the N=1, which took a considerable amount of time in order to be ready for submission of this revision, but it was indeed essential. We have also reworked the discussion sections where we further elaborate on the theoretical implications and potential limitations of our proposed framework, and suggest potential avenues of investigation for future research endeavors.

In sum, our findings are robust with the newly added analysis and have been compared against appropriate null models to ensure the validity of the results. Nevertheless, we have highlighted the limitation of this study.

Referee #1: social neuroscience (human), social perception

1. This manuscript attempts to explore the neural underpinnings of social facilitation in monkeys and humans. I find the manuscript interesting, with the potential to make a contribution to the literature. However, there are a number of limitations primarily with the theoretical motivation, research design, and statistical analysis that prevent me from recommending this version for publication. I discuss these below.

Author response: We acknowledge your interest and appreciate your concerns. We have now addressed the questions in the responses below to the best of our abilities.

2. There seems to be a conflation between detecting whether a conspecific is present (social presence) and having a conspecific present that affects performance on a task (social faiclitation/inhibition). These are not the same thing, but are treated as such in the introduction. The authors should clearly separate the perceptual mechanism from an attentional effect on

behaviour. My belief is that they are more interested in the latter, but frame the paper as exploring the former. This needs to be clarified.

Author response: We agree with the distinction pointed out by the reviewer. The fact is that in the literature on the effects of social presence in humans and nonhuman animals, the mechanisms related to the detection of presence and those related to the effects of this presence are not clearly differentiated. This blind spot deserves to be explored but was not the aim of the present study, which instead allows for advances on another front (the neural bases of social presence effects). The notion of “awareness of the presence of others” in the original version of our manuscript has therefore been removed to avoid confusions and better reflect the reality of the work conducted in the literature on social presence effects.

3. Why are hidden causal mechanisms at the synaptic level necessary to explain social facilitation effects? There is an implicit assumption that this is the right level of analysis without any evidence to support such an assumption. Please provide it.

Author response: The bottom-up framework presented in this manuscript was motivated by the dearth of investigations regarding the neurobiological underpinnings of social facilitation/inhibition (SFI) effects. Bayesian learning enables us to identify the distribution of parameters which best explain the observed trends of empirical data (or data features). It is indeed true that the dynamical models used in Bayesian learning possess an array of neurobiologically-informative parameters other than effective connectivity. However, a quick glance at the remainder of such parameters shows the potential unfeasibility of their involvement in social facilitation/inhibition. A good candidate parameter to explain this is rate/time constant of membranes/synapses in any of the presented generative models. The foundation of our work rests on the function of context-oriented neurons. These neurons are recorded in identical regions, and we possess no reliable information to infer their specific cell types. Therefore, the assumption of alteration in their rate constants can be not only unfeasible, but also implausible (as they can belong to a similar cell type, only differentially modulated via social context). It would therefore be more prudent and conservative to choose representations that describe and reduce an entire array of neurobiological phenomena, into a feasible, yet biologically-plausible set of parameters. This, in conjunction with the vast array of previous research on the significant role of effective connectivity (EC) alterations in attentional modulation (with the latter constituting the foundation of our proposed framework of SFI effects), formed the motivation for selecting EC as the proposed driver of SFI effects (see the introduction and discussion for the most influential research surrounding this topic). Finally, a genuine implementation of DCM is not a one-directional estimation of parameters, but a cyclic exploration of potential drivers through both model-based estimations and neurobiological investigations. It is therefore of utmost important to note that our aim has never been to conclusively champion EC changes as the only possible driver of social facilitation, but to rather kickstart the conversation and future investigations into SFI, which we believe is a central axis in social cognition.

4. The paragraph structure of the introduction makes it difficult to follow the argument. Single paragraphs are packed with numerous points on varied topics. I suggest a revision to the structure where one self-contained idea is present in one paragraph.

Author response: We have implemented major changes to both the introduction and discussion sections, and have attempted to present self-contained concepts in separate paragraphs, with appropriate transitions between said concepts.

5. The monkey data comes from a single monkey. I find this problematic for generalizability.

Author response: We initially precluded analysis of data from monkey M, due to the smaller nature of its dataset compared to monkey A, but completely agree with the reviewers on this. Though a time-consuming ordeal, –and starting with raw data– we conducted an identical preprocessing, analysis and inference pipeline on data obtained from monkey M. Despite the lower number of congruent/usable experimental sessions and categorized neurons, posterior estimation of synaptic efficacies in monkey M corroborates our initial findings with monkey A, the results of which can be accessed in a dedicated section in the appendix. We have chosen to separate the results of the two subjects (with the main body figures representing data from monkey A only) due to the aforementioned difference between the scale of their preprocessed data. With that said, and for thoroughness' sake, we pooled the empirical observations of the two subjects across both scales, and conducted another identical pipeline of Bayesian learning of synaptic efficacy (SE), the results of which again support our previous findings of increased excitatory synaptic efficacy. This pooled dataset was randomly permuted in order to conduct a similar inference pipeline for null-hypothesis testing (chance level).

6. The motivation for focusing just on executive control brain regions ACC and DLPFC in the monkey study is not clear to me. Why not sample neurons form across the social cognition brain network, including temporal lobe, prefrontal cortex, and precuneus?

Author response: Association-learning relies on feedback signals (Sutton and Barto, 1998). It is therefore possible that others' presence could affect learning through direct modulation of neural activity underlying learning and related behavioral performance. Said regions were therefore chosen as their neural activity has been shown to be tightly linked to the processing of feedback signals during learning, in conjunction with their involvement in attentional modulation (Asaad et al., 1998; Holroyd and Coles, 2002, 2008; Nieuwenhuis et al., 2004; Amiez et al., 2006; Kennerley et al., 2006; Kobayashi et al., 2006; Kennerley and Wallis, 2009). In addition, the investigation was conducted longitudinally across several years, with invasive recording of neurons limited to these two adjacent regions. Since the *in vivo* electrophysiology technique is particularly time-consuming (electrodes are inserted transdurally every day and moved to locate the desired cellular activity), a potential solution would have been the chronic implantation of electrode arrays in several regions. This solution has the advantage of not requiring time at the beginning of a recording session to search for the appropriate recordings. However, the use of electrode arrays has a number of limitations (e.g. implant lifespan; Lara Merken et al 2022 J. Neural Eng. 19 066039), including a major one, which is the limited length of the electrode stems, preventing the study of cortical areas buried in the sulci or in deeper regions of the brain, such as the ACC, the temporal lobe, the precuneus, or the orbitofrontal cortex. For these reasons, the number of potential regions that can be recorded simultaneously over the long term is not feasible. Furthermore, the literature on the social brain has identified regions that are involved in processing so-called social information (as the reviewer also pointed out). On this basis, a recurrent debate about the social brain is whether identical, different, or partly overlapping neuronal representations support the processing of social and non-social information (see for a review: Ruff and Fehr, 2014). However, this debate neglects the possibility that the processing of both types of information (social or not) may rely on neurons whose activity significantly increases under social presence (social neurons as those mentioned here). This is what Demolliens et al. 2017 found and here we provide the first evidence that the presence of a conspecific increases synaptic connectivity among these neurons. The theoretical and clinical implications of our findings are now more extensively presented in the general discussion section of the manuscript.

7. In social facilitation studies, the conspecific is often engaged in the task as well rather than being a mere observer. Would the pattern of results change if the actor believed that they could socially offload (see Tufft & Richardson, 2020) onto the conspecific because they are also engaged in the task?

Author response: A conspecific engaging with the task typically falls under overt social interaction (e.g. cooperation). We specifically designed the tasks so as to preclude/inhibit any possibility of such interaction/offloading, since social facilitation is exclusively defined as the elevations to task performance under 'mere' presence of conspecifics. This means that the conspecific should only bear the role of a simple spectator, and nothing more. However, if such overt interaction was allowed within the context of the experiments (which to reiterate, are not possible in our implementations), then indeed we could potentially observe an entirely different trend with regards to modulations of task performance. The effects of coaction (the presence of other individuals engaged in the same task but independently of one another) have also been studied, but in the social presence literature these devices also exclude any communicative interaction or cooperation between the individuals present. Coaction devices are nevertheless more difficult to implement and also complicate interpretations, since coaction often generates not only presence effects but also effects related to competition and social comparisons, at least in primates.

8. I understand the desire to focus on attention, but why restrict the EEG analysis just to the alpha band? There are potentially interesting results in the other bandwidths that were filtered out.

Author response: We focused solely on alpha-band activity, not only due to the prominence of alpha peak in the vast majority of the participants (see a dedicated section in the discussion for a more detailed explanation), but also since it is strongly associated with bottom-up feature processing, distractor suppression, top-down attentional control, and selective attention (Jia et.

al., 2021, Magosso et. al., 2019, Lobier et. al., 2018). Equally important, this oscillatory band has been strongly associated with large-scale network integration, which we aimed to employ as our chosen empirical data feature in the mesoscale inference of synaptic efficacies (Chapeton et. al., 2019).

Referee #2: human neuroscience, computational neuroscience, Bayesian modeling, DCM

This paper investigates how the mere presence of another individual alters attention-related neural dynamics and improves task performance. Drawing from experiments in both non-human primates and human participants, the authors propose that "social facilitation" arises partly through enhanced excitatory synaptic efficacy. They combine behavioral testing (an association-learning task in monkeys and a visuomotor interception task in humans) with advanced computational modeling at three levels of brain organization: (a) single neurons (micro), (b) cortical columns (meso), and (c) large-scale neural networks (macro). Their central finding is that social presence can strengthen connectivity in attention-oriented circuits across these scales, particularly by boosting recurrent excitatory connections, ultimately correlating with improved behavioral performance for certain groups (notably female participants in the human study).

This paper bridges single-cell recordings, local field potentials, and whole-brain EEG networks, offering a comprehensive account of how social presence might act at different levels of neural organization. The authors use well-controlled experimental designs in both monkeys (isolating mere presence vs. absence) and humans (observer vs. no-observer conditions). Here are some aspects of the paper that when addressed could improve the paper:

MAJOR:
1. Limited Neural Sampling in Monkeys: While the monkey data offer valuable micro- and mesoscale perspectives, effectively only one monkey's neural recordings were analyzed in detail (the second had data-quality issues). Such an N=1 for electrophysiological results raises concerns about individual variability. Only dlPFC and ACC were studied in-depth; no data exist for other areas that might also be sensitive to social presence (e.g., sensory cortices or subcortical arousal systems).

Author response: As alluded to in our response above to Reviewer I, we initially precluded analysis of data from monkey M, due to the smaller nature of its dataset compared to monkey A, but completely agree with the reviewers on this. Though a time-consuming (but essential) ordeal, –and starting with raw data– we conducted an identical preprocessing, analysis and inference pipeline on data obtained from monkey M. Despite the lower number of congruent/usable experimental sessions and categorized neurons, posterior estimation of synaptic efficacies in monkey M corroborates our initial findings with monkey A, the results of which can be accessed in a dedicated section in the appendix. We have chosen to separate the results of the two subjects (with the main body figures representing data from monkey A only) due to the aforementioned difference between the scale of their preprocessed data. With that said, and for thoroughness' sake, we pooled the empirical observations of the two subjects across both scales, and conducted another identical pipeline of Bayesian learning of synaptic efficacy (SE), the results of which again support our previous findings of increased excitatory synaptic efficacy. This pooled dataset was randomly permuted in order to conduct a similar inference pipeline for null-hypothesis testing (chance level).

2. Differences Between Monkey and Human Tasks: The monkey association-learning task and the human interception task differ significantly in cognitive demands, which could limit cross-species comparisons. Although both tap into attentional processes, the tasks engage distinct motor and cognitive routines.

Author response: Indeed, the most optimal multiscale social facilitation/inhibition (SFI) study should entail closely-matched tasks across species. However, social facilitation reportedly persists across tasks and species. Therefore, given the shared visuospatial nature of both tasks, the constraints of simple/well-learned experimental configurations, and the necessity of attentional modulation for achieving success across trials, one can assume the involvement of similar underpinnings (with regards to attentional modulation) in both. For the purposes of this investigation, the tasks were carefully chosen to fulfill all essential criteria of an SFI study, with their design differing simply due to the availability of experimental apparatus and the central focus of the experimental institutions at the time of their conceptualization (Aix-Marseille University, and University Medical Center Groningen). The fact that the conclusions remain essentially the same in humans and nonhuman primates faced with different tasks also helps increase the external validity of our findings.

3. Sample Characteristics and Generalizability: In humans, the authors tested 27 participants split by sex. While they uncovered an intriguing sex difference, women showing clear facilitation, men not, the modest sample size calls for caution. Null results in the male group could reflect insufficient power or unexamined psychosocial factors (e.g., stress responses).

Author response: We concur with this limitation of the lateral-interception task. During the design and conductance of the study, we took extra care to control for factors such as sex, age and occupation, with our initial hypothesis revolving around absence of any differences in performance or functional connectivity measures across the subject groups. When it comes to analysis of mere presence effects across subject groups, SFI investigations –by definition– call for an expansive participant pool (or alternatively within-group longitudinal investigations, as with the association-learning task). Moreover, SFI is first and foremost defined through modulations of task performance across conditions. As such, even with the presence of similar behavioral trends across groups, disparate scales of inter-individual variability across samples, in conjunction with a relatively small sample size can compound the inference of genuine group-level statistics. Consequently, we caution readers to not associate the between-group differences outlined here with an inherent and prevalent disparity of facilitation/inhibition capacity across other tasks.

4. Stability of Parameter Estimates: Although the authors use advanced Bayesian inference techniques, they do not thoroughly address how the inferred parameters (e.g., synaptic gains at each scale) are under slight variations in the dataset or modeling choices. Such an analysis would increase confidence that small changes in sampling or data quality do not substantially alter their inferences.

Author response: Thank you for pointing this out. Indeed, for each scale, we first conducted in-silico validation to address this concern and assess the degeneracy and identifiability of the parameters. We have now added sensitivity analyses using chi-squared error criterion (Fig S10) for the three scales, which demonstrate the confidence level in identifying the parameters. Importantly, the posterior shrinkage observed in our results indicates the reliability of the estimations. Additionally, we have compared the inferred posterior distributions with those obtained under a null model to further validate the specificity and informativeness of our results (Fig S11).

5. Interpretation of Sex Differences: The study highlights that female participants showed increased effective connectivity in attention networks under observation, whereas males did not. Possible explanations (e.g., motivational or arousal differences) receive only brief mention, and deeper exploration of relevant literature (e.g., gender differences in stress or social facilitation) would help clarify why these effects emerged.

Author response: The revised limitation section in the discussion now has a dedicated section, where we elaborate on various factors which could have led to the observation of this group-based trend. In short: rather than stemming from sampling effects, the lack of facilitation of performance during conspecific presence in the male subject group might partially stem from group-based differences such as the level of perceived rank within the immediate social environment (in this case, the task space; Balconi et. al., 2015). Said absence of performance modulation could also be explained by recent findings on sex differences in social cognition, such as women exhibiting greater empathy, positive evaluation of face, and interest in social information compared to men (Proverbio AM., 2021, Proverbio AM., 2016).

MINOR:

Some methodological details (such as EEG source localization or the rationale for kinematic measures) appear mid-results rather than in a separate Methods section, occasionally disrupting the narrative flow.

Author response: We have moved the explanation of the kinematic measures to the methods section. However, we are unable to find where we go into details of source-localization (in the main text) other than the methods section.