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Report

Frequency-Dependent Enhancement of Fluid Intelligence Induced by Transcranial Oscillatory Potentials

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Summary

Everyday problem solving requires the ability to go beyond experience by efficiently encoding and manipulating new information, i.e., fluid intelligence (G*f*) [1]. Performance in tasks involving G*f*, such as logical and abstract reasoning, has been shown to rely on distributed neural networks, with a crucial role played by prefrontal regions [2]. Synchronization of neuronal activity in the gamma band is a ubiquitous phenomenon within the brain; however, no evidence of its causal involvement in cognition exists to date [3]. Here, we show an enhancement of G*f* ability in a cognitive task induced by exogenous rhythmic stimulation within the gamma band. Imperceptible alternating current [4] delivered through the scalp over the left middle frontal gyrus resulted in a frequency-specific shortening of the time required to find the correct solution in a visuospatial abstract reasoning task classically employed to measure G*f* abilities (i.e., Raven's matrices) [5]. Crucially, gamma-band stimulation (γ-tACS) selectively enhanced performance only on more complex trials involving conditional/logical reasoning. The present finding supports a direct involvement of gamma oscillatory activity in the mechanisms underlying higher-order human cognition.

Results

We aimed to improve fluid intelligence (G*f*) in healthy subjects by using transcranial alternating current stimulation (tACS), a noninvasive brain stimulation methodology shown to be effective in the frequency-specific modulation of regional cortical activity. In analogy with animal evidence [6], it has been suggested that tACS may induce entrainment of endogenous brain rhythms in humans, thereby modulating the functions associated with synchronized activity in the underlying neural networks [3]. This effect has been described for the motor [7–9], visual [10], and somatosensory [11] domains, and initial evidence supports its involvement in higher functions, such as decision-making [12] and working memory [13] processes.

Twenty tACS-naive, right-handed, healthy volunteers underwent tACS over the left middle frontal gyrus (MFG) while performing an extended version of Raven's matrices [5], which allowed reliable repeated assessments of performance in this classic test of G*f* abilities. MFG is a key component of a processing module that sustains abstract reasoning in a largely modality-independent manner; its activation has been reported in both visuospatial and verbal analogical reasoning tasks [14] that require one to move beyond perceptual relations into complex abstractions by integrating meaningful logical relationships while inhibiting irrelevant information [2]. MFG activation is crucial in tasks involving the high level of abstraction required by logical conditional arguments (e.g., where specific rule of inference "modus tollens" is applied: if P then Q; not Q; "If there is a circle, then there is a triangle. There is not a triangle. Therefore, there is not a circle"; Figure 1A, LOGIC). On the other hand, activation is minimal when simple perceptual relations need to be inferred (i.e., linear arguments as those in relational syllogisms, e.g., P is to the left of Q; Q is to the left of R; "The circle is to the left of the triangle. The triangle is to the left of the square. Therefore, the circle is to the left of the square"; Figure 1A, REL), which seems to rely on posterior areas, such as the temporal-parietal-occipital junction [15]. The solution of specific Raven's matrices involves variable degrees of the two processes. Accordingly, by applying a prefrontal stimulation, we expected to differently affect performance in relational, perceptual trials and in more complex logic trials.

We assessed response times (RTs; i.e., the time required to solve each matrix) and accuracy in trials of different complexity that tackled, in a fully randomized manner, relational and conditional abstract reasoning (namely, matrices with one, two, or three relations or logic trials). We aimed to address the frequency-specific effect of stimulation within the main physiological brain rhythms by comparing performance during four tACS conditions—5 Hz (θ band), 10 Hz (α band), 20 Hz (β band), and 40 Hz (γ band)—and a placebo, sham stimulation. Details of the experimental procedures and tACS parameters are reported in Figure 1 (see also Supplemental Experimental Procedures available online).

Data-Driven Relations across Trial Types

The overall pattern of accuracy and RTs was consistent with the hypothesis that the solution of the two different trial types involves at least partially separable resources (Figure 1D). More specifically, the longer RTs required to solve logic matrices cannot be accounted for by a greater difficulty along the same dimension as relational trials. In the solution of relational trials, we observed a linear additive cost of each relation of ~5 s, with highly correlated individual performance (one versus two relations: $r = 0.81$; one versus three relations: $r = 0.69$; $p < 0.001$), while no correlation was observed with RTs in logic matrices (logic versus three relations: $r = 0.12$; not significant). On the other hand, error rates were less effective in differentiating trial types, with comparable accuracy in logic and the most difficult relational trials and increased shared variability across trial types.

tACS Effect on Abstract Reasoning

A clear frequency-specific effect emerged, as performance was significantly affected only by γ-tACS. Importantly, the time required to produce correct responses was affected by

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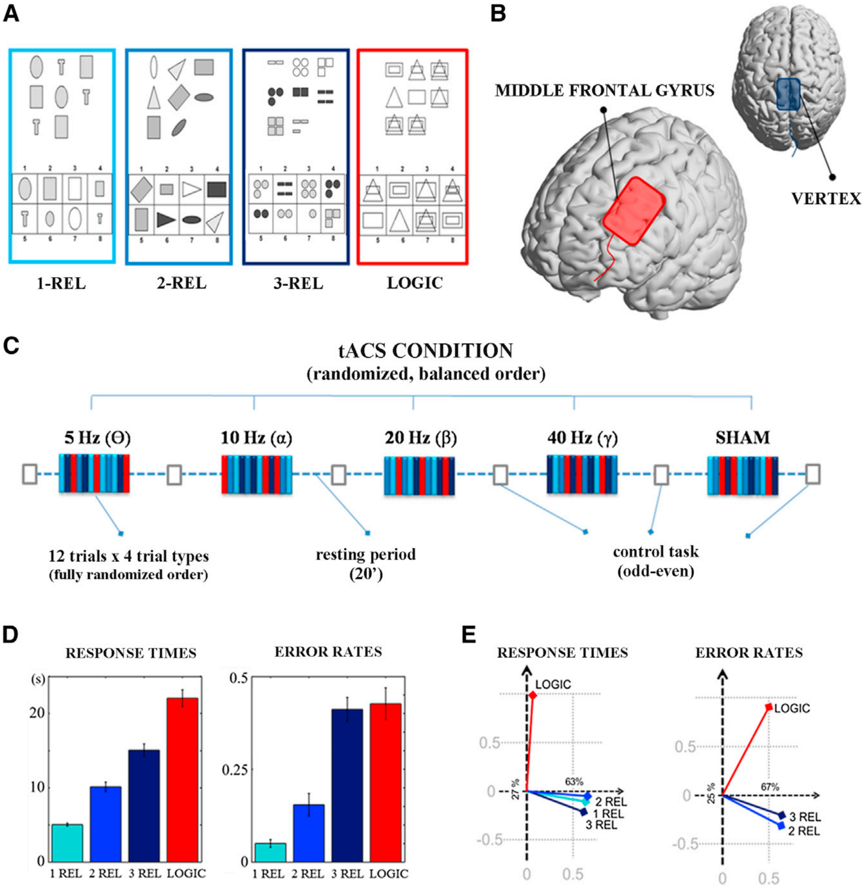

Figure 1. Task, Stimulation, and Performance

(A) Each matrix was composed by an upper part containing a 3 × 3 stimuli grid. Subjects were asked to report which of eight objects listed underneath would complete the series by filling the bottom right blank cell. The correct response, which had to be given as fast as possible, could be inferred either by capturing *relations* across objects (i.e., the one, two, or three features along which objects varied across the matrix) or by performing *logic* operations (i.e., conjunction, disjunction, or exclusive disjunction) across the grid.

(B) Stimulating electrodes were positioned according to the International 10–20 EEG System: the "active" electrode was centered on the left middle frontal gyrus ($x = -34$, $y = 16$, $z = 30$), whereas the "reference" electrode was placed on Cz (vertex).

(C) Experimental sketch. During each tACS condition, accuracy and response times were acquired for 48 matrices (12 of each of the four types), which were randomly presented. A maximum of 60 s was allowed to solve each matrix. A resting period (20 min) was allowed between presentations, during which subjects performed a low-cognitive-load disengaging task without stimulation.

(D) Mean error rates and accurate response times. Logical reasoning is a costly process: in order to match the accuracy observed in the solution of three-relations tasks, the solution of logic subtests requires longer response times (raw means ± SE).

(E) Data-driven relations across trial types. Principal component analysis offers a straightforward depiction of the observed correlation structure (unrotated solution, analysis on correlation matrix of individual averages): the orthogonal distribution for relational and logical subtests suggests that individual variability in response times arises from heterogeneous processes across tasks. For mean error rates, a higher correlation along the first component was observed (coefficients for all variables > 4, logic and three-relations raw correlation: $r = 0.46$, $p = 0.032$). Error rates for one-relation matrices were omitted because of ceiling performance and no meaningful contribution to variance.

γ-tACS in a trial-type-specific manner, pointing to a specific improvement of the conditional reasoning abilities required to solve logic trials. Regression analyses (generalized estimating equations, gamma regression, loglog link; see also Supplemental Analyses) [16] with tACS conditions and trial type as predictors yielded a highly significant estimation of the interaction terms (tACS × trial type $\chi^2 = 42.2$, $p < 0.001$; tACS $\chi^2 = 4.15$, $p = 0.386$; task $\chi^2 = 1{,}614.72$, $p < 0.001$). Pairwise comparisons of active tACS versus sham conditions highlighted that the source of interaction was faster RTs in the logic subtests during γ-tACS (mean difference = -3.2 s, $p = 0.001$, corrected; Figures 2A and 2B; see also Figure S1). No other differences were significant. Analysis of error rates did not show significant interactions (logistic regression: tACS × task $\chi^2 = 12.7$ $p < 0.122$; tACS $\chi^2 = 1.84$, $p = 0.786$; task $\chi^2 = 138.68$, $p < 0.001$) or pairwise differences. In spite of training, both accuracy and RTs showed an order effect, yielding to slower and less accurate responses on the first presentation, regardless of tACS condition. The order of tACS conditions was balanced in our experimental design. Furthermore, adding this factor to the model improved overall goodness of fit but did not change the results for the effects of interest.

Pairwise Comparisons

T scoring of the differences from sham stimulation was employed as a straightforward way to represent and compare effects. All pairwise tACS condition × trial type contrasts have been explored. The only significant differences (least-significant difference test correction for multiple comparisons) within the same trial type were observed for RTs in the logic trial type, with correct responses during γ-tACS being faster than in the sham ($p = 0.023$), θ-tACS ($p = 0.012$), α-tACS ($p = 0.043$), and β-tACS ($p = 0.041$) conditions.

Control Analysis 1: Lack of Effect on Speed/Accuracy Trade-Off

The observed improvement in speed induced by prefrontal γ-tACS during logic-based reasoning did not occur at the expense of accuracy. Parametric analysis of RTs in error trials did not show significant differences (main effect of tACS in logic trials: $\chi^2 = 1.7$, $p = 0.78$). This observation was confirmed by inspection of empirical distributions (Figure 3A). Moreover, the likelihood of having a "fast" response in accurate trials (where "fast" is defined as faster than median RT over both correct responses and error) did not differ across tACS conditions. As a matter of fact, during γ-tACS, we observed a nonsignificant tendency ($\chi^2 = 4.8$, $p = 0.306$) toward an increased occurrence of fast and accurate responses; this is not consistent with a change in speed/accuracy trade-off, which would have made responses faster but less accurate.

Control Analysis 2: Lack of Effect on Task Switching

The employed presentation of matrices in a random sequence differs critically from the standard practice of presenting

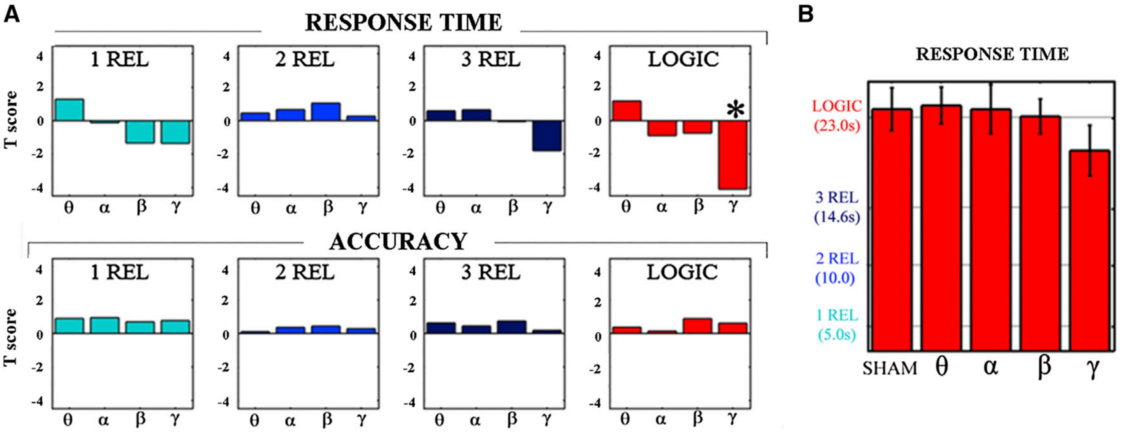

Figure 2. tACS Effects

(A) tACS versus sham: T score. Response times on accurate trials were significantly faster when subjects received γ-tACS, specifically in the solution of matrices involving logical reasoning. No difference from sham stimulation was observed in the extrapolation of relational rules (pairwise comparisons of transformed accurate response times, tACS versus sham, *$p = 0.001$, corrected). Accuracy did not differ across conditions (bottom row). See also Figure S1 for details of data distribution.

(B) Mean response times for accurate responses in logic trials across tACS conditions. On the y axis, mean response times in the four different trial types are shown for reference (raw means ± SE). During γ-tACS, response times appear halfway between responses related to three-relations trials and responses related to logic matrices without stimulation, which corresponds to an improvement of about 15%.

Raven's matrices in order of progressive complexity [5]. This approach possibly reduced the confounding role of learning and other possible effects related to presentation order. However, such adaptation also introduced the need to frequently switch between relational and logic trials. It has long been known that task set reconfigurations are accompanied by slower responses, and recent evidence points to the involvement of prefrontal areas [17] that could have been secondarily affected by tACS. Nonetheless, performance did not benefit from repetition of logic or relational tasks (regression analysis: lack of main effect of preceding task, $\chi^2 = 0.39$, $p = 0.55$, or preceding task × task interaction, $\chi^2 = 0.18$, $p = 0.67$). This suggests that the observed effect cannot be interpreted as a reduction of task-switching costs; rather, it is more directly related to the specific processes underlying logical reasoning.

Control Experiment 1: Attention and Tiredness Monitoring Task

As shown in Figure 1B, participants were asked to perform a brief (4 min) task in rest periods between each block of matrices (six sampling in total). Subjects were asked to categorize as odd or even 50 randomly generated numbers. Such a simple task (accuracy was steadily at ceiling level: ~98%, $\chi^2 = 0.57$, $p = 0.96$) allowed disengagement from the main task while monitoring, through reaction times, potential effects of reduced attention and fatigue throughout the experiment. It should be noted that while the balanced order of tACS condition controlled for within-experiment effects, it was not possible to exhaustively explore possible aftereffects of one specific condition on the following. However, preceding and following tACS conditions did not affect RTs ($\chi^2 = 1.57$, $p = 0.81$; $\chi^2 = 2.86$, $p = 0.58$) (Figure 3B). This evidence, together with lack of effects on relational tasks, makes the existence of this confounding factor unlikely.

Discussion

Current findings show that healthy participants receiving rhythmic imperceptible currents at gamma band on the left prefrontal cortex became about 15% faster in correctly solving complex Raven's matrices, a widely used neuropsychological instrument indexing fluid reasoning [18]. Besides being frequency specific, the improvement was crucially dependent on task complexity since only logic trials were affected. These findings possibly suggest a causal involvement of gamma-oscillatory activity in the neural processes underlying higher-order human cognition, a novel finding partially contrasting the view of high-frequency synchronization as an epiphenomenon of neuronal activity [6]. These results are of relevance in view of the difficulty of manipulating individual logic abilities, a key but still elusive target for cognitive rehabilitation.

There is a general agreement that G*f* represents a stable individual trait, since it is considered resilient to influences of education, socialization, drugs, and behavioral training [19, 20], with few exceptions [21]. Neuroimaging evidence indicates a limited number of brain regions supporting abstract reasoning abilities: logic tasks are associated with different levels of activation in frontal and parietal areas, and frontal involvement increases with task difficulty [22–24]. After initial engagement of parietal regions, believed to sustain perceptual processing, the online manipulation of information is accompanied by specific prefrontal activations [25, 26], with a crucial role played by the MFG for inferential processes based on conditional arguments, when the inhibition of irrelevant information is also required. Our trial-type-specific effect supports the specific role of this brain region in demanding logical processing. However, possible spread of current over neighborhood regions (i.e., superior and inferior frontal gyrus) due to the size of the stimulating electrode cannot be excluded.

Brain activity underlying fluid reasoning has not been directly investigated with high-time-resolution methodologies such as electro- or magnetoencephalography. However, there is general convergence in assigning to high-frequency synchronization a role in the large-scale coordination of activity relevant for cognition, such as optimizing stimulus processing [26], neural binding [26], and cognitive control of input processing [27, 28]. Consequently, and in analogy with its

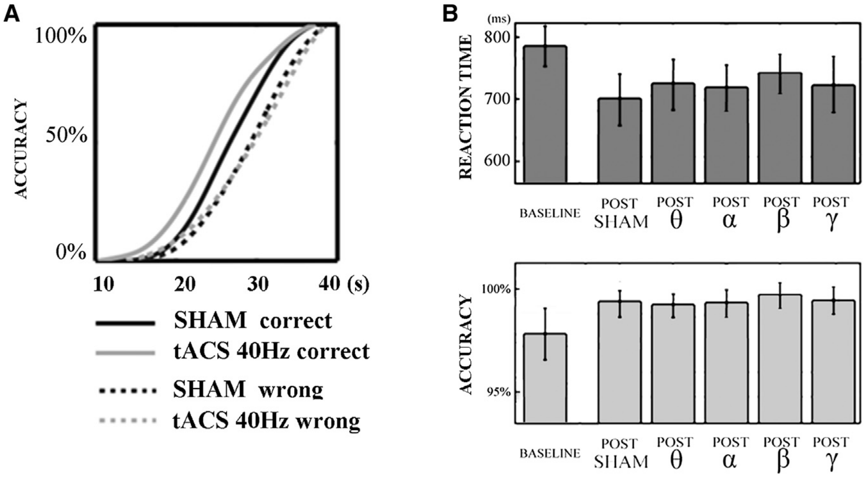

Figure 3. Lack of tACS-Induced Changes in Speed/Accuracy Trade-Off and Vigilance Monitoring

(A) Empirical cumulative distribution of response times during sham and active tACS. The enhancement of performance induced by γ-tACS (i.e., the left-side shifting of the rising solid curve) does not derive from changes in speed/accuracy trade-off, as wrong responses (dashed lines) are unaffected by stimulation.

(B) Mean accuracy and reaction time during the vigilance/fatigue monitoring, "odd/even task" (raw means ± SE). Each block is referenced to the preceding tACS condition, aside from the baseline block that was executed at the very beginning of the experiment. Reaction times did not differ ($\chi^2 = 1.57$, $p = 0.81$; $\chi^2 = 2.86$, $p = 0.58$) (upper panel), and accuracy was stably at ceiling level (~98%, $\chi^2 = 0.57$, $p = 0.96$) (lower panel) throughout the poststimulation blocks. Worse performance at the baseline captures a minor order effect, possibly due to initial lack of familiarity for the stimulus-response mapping for this easy task. This effect was effectively suppressed by the balanced order of tACS condition, consistent with lack of tACS-specific aftereffects.

involvement in a wide range of higher-order cognitive functions like attention [29], memory [30], language [31], and learning [32], gamma activity might also be involved in the orchestration of prefrontal activity related to fluid intelligence. In the current study, indeed, participants selectively reduced the time needed to correctly solve each logical matrix, suggesting that gamma-band entrainment may lead to the optimization of local information processing.

We speculatively interpret the observed effect to indicate that a beneficial effect of tACS could rise from entrainment of endogenous rhythms. While this view is supported by initial animal evidence [8], the very mechanism underlying the effects is unknown and possibly frequency and task specific. Models of gamma activity emphasize the importance of timing, while tACS phase is agnostic to both underlying neural processing and stimuli presentation. From this perspective, the observed effect could be either a positive modulation achieved by mechanisms other than entrainment or the outcome of a negative modulation of processes detrimental to performance. Conclusive evidence awaits future studies combining recording and stimulation techniques.

Nonsinusoidal transcranial random noise stimulation (tRNS) has been shown to increase cortical excitability only when delivered at high frequencies [33, 34]. This evidence suggests that the frequency specificity of the present finding would depend on gamma being the highest explored frequency. Most importantly, it has been recently demonstrated that high-frequency tRNS may also enhance the performance in higher-order cognitive tasks like arithmetic calculation learning [35]. This might be due to a change in cortical excitability within the stimulation site, achieved through an amplification of subthreshold oscillatory activity due to a stochastic resonance effect, which is a possible alternative explanation for the frequency-specific entrainment phenomenon we are supporting here. Even though the effects of tRNS are reported only for stimulation over 100 Hz, and similar effects were not observed for both periodic and aperiodic stimulations closer to the gamma frequency we used [34], we consider such an interpretation to be a plausible alternative and thus worthy of further investigation.

Complex, time-demanding tasks can be hypothesized to involve a decision step in which commitment to a response is delayed by revision and further comparison of candidate solutions. Interference with such a process could likely reduce response time and provide an alternative explanation for the reported effect. However, the lack of changes in speed/accuracy trade-off suggests that the inhibited process is functionally irrelevant and makes this alternative view less likely when subjects are trying to respond, as in our experiment, as quickly and as accurately as possible. We also consider it unlikely that the observed effect was secondary to boosting of the working memory process, which is thought to contribute to G*f* [21] and can be transiently improved by phase-locked parietoprefrontal θ-tACS [13]. However, (1) both test matrices and possible solutions were always available to subjects' sight, thereby making the working memory load of the task negligible, and (2) as previously demonstrated, γ-tACS did not affect working memory [13], and we did not find any performance change during tACS applied at θ frequency, the prevailing oscillatory activity accompanying working memory operations at the prefrontal level [36].

Theoretically, additional refinements regarding tACS application might consider a finer individual tuning of the frequency of stimulation, taking into consideration the variability of the gamma-band activity (i.e., from 30 to 70 Hz) [37, 38]. This could even magnify the observed effects, since we used a single gamma frequency.

Finally, aside from the limit to interpretation and the potential relevance to cognitive rehabilitation, the present findings might represent a conceptual advance in the understanding of the neural signatures underlying fluid intelligence and are the first evidence supporting the causal involvement of high-frequency brain synchronization in human cognition [39], thus contrasting with views of gamma-band activity as a mere byproduct of neuronal activity [6].

Supplemental Information

Supplemental Information includes one figure, Supplemental Analyses, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.06.022.

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