

1 **Analysis of the effectiveness of sub-sensory electrical noise stimulation during**
2 **visuomotor adaptations in different visual feedback conditions**

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4 *Running Title: Effect of Stochastic Resonance on Visuomotor Adaptations*

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22 **Abstract**

23 Sub-sensory electrical noise stimulation has been shown to improve motor performance in tasks that rely
24 principally on proprioceptive feedback. During the generation of movements such as reaching,
25 proprioceptive feedback combines dynamically with visual feedback. It is still unclear whether boosting
26 proprioceptive information in tasks where proprioception mixes with vision can influence motor
27 performance at all, either by improving or worsening it. To better understand this point, we tested the effect
28 of electrical noise stimulation applied superficially to the muscle spindles during four different experiments
29 consisting of isometric reaching tasks under different visual feedback conditions. The first experiment
30 (n=40) consisted of a reach-and-hold task where subjects had to hold a cursor on a target for 30 seconds
31 and had visual feedback removed 10 seconds into the task. Subjects performed 30 repetitions of this task
32 with different stimulation levels, including no stimulation. We observed that trials in which the stimulation
33 was present, displayed smaller movement variability. Moreover, we observed a positive correlation between
34 the level of stimulation and task performance. The other experiments consisted of three versions of an
35 isometric visuomotor adaptation task where subjects were asked to reach to random targets in less than 1.5
36 seconds (otherwise incurring in negative feedback) while overcoming a 45° clockwise rotation in the
37 mapping between the force exerted and the movement of the cursor. The three experiments differed in the
38 visual feedback presented to the subjects, with one group (n=20) performing the experiment with full visual
39 feedback, one (n=10) with visual feedback restricted only to the beginning of the trajectory and one (n=10)
40 without visual feedback of the trajectory. All subjects performed their experiment twice, with and without
41 stimulation. We did not observe substantial effects of the stimulation when visual feedback was present
42 (either completely or partially). We observed a limited effect of the stimulation in the absence of visual
43 feedback consisting in a significant smaller number of negative-feedback trials in the first block of the
44 adaptation phase. Our results suggest that sub-sensory stimulation can be beneficial when proprioception
45 is the main feedback modality but mostly ineffective in tasks where visual feedback is actively employed.

46 **Keywords:** proprioception; visual feedback; stochastic resonance; visuomotor adaptation

47 **1. Introduction**

48 Mechanical and electrical noise stimulation targeting joints and muscles can alter the kinesthetic
49 sense and lead to improved motor performances (Cordo et al., 1996; Gravelle et al., 2002; Priplata et al.,
50 2002; Collins et al., 2003; Priplata et al., 2006; Ross and Guskiewicz, 2006; Mendez-Balbuena et al., 2012;
51 Collins et al., 2014; Iliopoulos et al., 2014; Miranda et al., 2016; Severini and Delahunt, 2018). Mechanical
52 noise stimulation directly modifies the response of sensory receptors, while electrical noise stimulation
53 alters the baseline transmembrane potential of the stimulated afferents making them more likely to fire in
54 response to a weak stimulus (Gravelle et al., 2002; Miranda et al., 2016). Both effects are supposedly related
55 to stochastic resonance (SR), a phenomenon for which noise can improve the reception of weak signals in
56 threshold-based systems (Gammaitoni, 1995). By the SR phenomenon, noise added to the input of a
57 threshold-based receiving system can improve the detection of a weak input signal by spuriously amplifying
58 it. Values of noise that are too low may not bring the weak signal above the receiving threshold, while
59 values of noise that are too high risk to mask the characteristics of the input signal and thus lead to erroneous
60 detections. Therefore, the SR phenomenon predicts the presence of an optimal level of stimulation that
61 maximizes the performance of the receiving system.

62 The SR phenomenon has been observed to occur in response to noise stimulation in biological
63 systems in general (Collins et al., 1995), and in human sensory receptors in particular (Cordo et al., 1996;
64 Mendez-Balbuena et al., 2012; Iliopoulos et al., 2014; Mendez-Balbuena et al., 2015). Proprioception plays
65 a crucial role during the execution and learning of voluntary movements (Fleishman and Rich, 1963; Sober
66 and Sabes, 2003) and sensory deficits have been shown to affect motor re-learning after a neurological
67 injury (Vidoni and Boyd, 2009). Several studies have shown that superficial electrical noise stimulation
68 targeting sensory receptors at sub-sensorial current levels (intended as current levels that do not elicit
69 conscious perception) can improve performance during different motor tasks in healthy subjects
70 (Magalhaes and Kohn, 2012; Iliopoulos et al., 2014; Magalhaes and Kohn, 2014), elderlies (Gravelle et al.,
71 2002) and individuals suffering from sensory loss (Collins et al., 2014). In all these experiments, the motor

72 tasks selected (i.e. single leg stance) relied heavily on proprioception as sensory feedback modality.
73 Recently, we were also able to show that, in opposition to the results obtained using sub-sensorial
74 stimulation, supra-sensorial currents lead to a decrease in motor performance during mildly challenging
75 balance tasks (Severini and Delahunt, 2018), although it is not clear whether this effect is caused by the
76 conscious sensation or by the degradation in performance expected by the SR model for levels of noise
77 above the optimal one. It has been proposed that sub-sensory noise stimulation could be used to improve
78 the quality and quantity of available proprioceptive information during rehabilitation of patients affected
79 by proprioceptive deficits (Collins et al., 2003). In this scenario, since motor learning in rehabilitation is
80 often associated with complex tasks (e.g. walking, reaching...) where several sensory feedback modalities
81 are integrated and employed at the same time, it is paramount to understand how boosting proprioception
82 can affect the overall feedback information. This latter point is still unexplored in literature. In fact, while
83 most studies employing sub-sensory stimulation have shown its benefits in tasks where proprioception is
84 the main feedback modality, it is not clear what its effect would be in tasks where proprioception integrates
85 (or competes) with other sensory modalities, such as visual. As a case in point, during reaching movements
86 proprioceptive and visual feedback (VF) are weighted flexibly depending on the task and on the quality and
87 availability of feedback (Sober and Sabes, 2003; 2005). In this perspective, externally altering the natural
88 “gain” of proprioception through sub-sensorial stimulation could affect the sensory weighting that happens
89 during the task and impact motor performance. It cannot be excluded also that the weighting process could
90 completely “bypass” the artificial sensory boost.

91 In this work we aim at testing if enhancing proprioception through sub-sensorial electrical
92 stimulation can alter motor performance during reach-and-hold and visuomotor adaptations (VMA) tasks
93 with different VF conditions. As motor adaptation is considered one of the processes constituting motor
94 learning (Shadmehr and Wise, 2005; Krakauer, 2009), our experiments aim also at giving additional
95 information on the usability of SR stimulation as an additional aid during rehabilitation therapy of reaching

96 movements. In our experiments, we asked subjects to perform a reach-and-hold task where VF was removed
 97 during the hold part of the task. Subjects repeated the task several times with different levels of sub-sensorial
 98 stimulation applied to the muscles driving the movement. This experiment was designed for determining
 99 the subject-specific optimal stimulation level, defined as the current level minimizing movement variability
 100 during the hold phase of the movement when VF was not present (thus in the portion of the task that was
 101 only reliant on proprioceptive feedback). Subjects were then split in three groups and each group performed
 102 a version of a visuomotor adaptation experiment twice, once with optimal sub-sensory stimulation (*Stim*
 103 condition) and once with no stimulation (*NoStim* condition), in a random order. One group performed the
 104 experiment with the VF always present (*Full VF*), one with VF limited to the initial part of the reaching
 105 movement (*Limited VF*) and one with VF only of the starting positions and end results of each movement
 106 (*No VF*). These three VF conditions were selected to examine the impact of enhancing proprioception in
 107 both the planning and on-line adjustment phases of the movement. We report here a limited effect of sub-

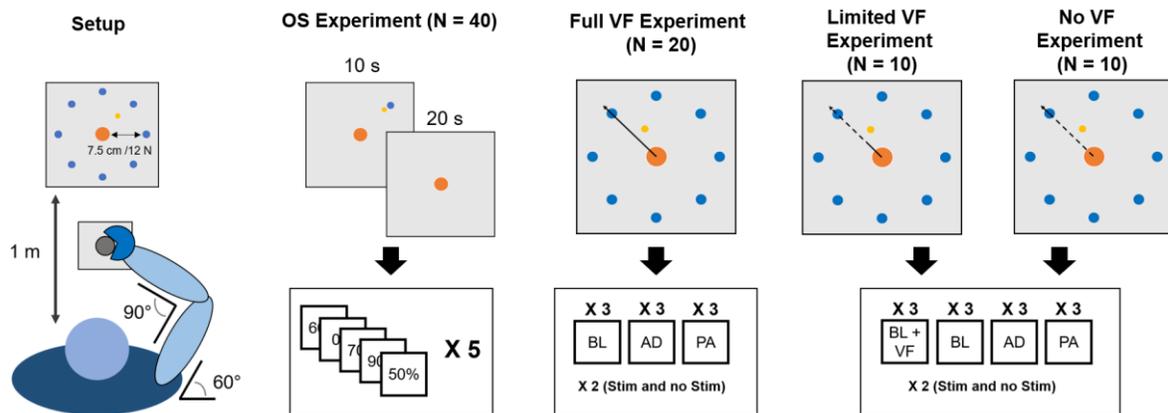


Figure 1. Experimental Setup. Subjects maintained the same position (leftmost panel) through all the experiments. During the OS experiment subjects had visual feedback during the reaching part of the trial and the first 10 seconds of holding and no visual feedback for the remaining 20 seconds. In the VMA experiments, visual feedback (bold line marks when it is present, dashed line when it is absent) changed across the different versions of the experiment. In the Full VF version feedback was always present. In the Limited VF version feedback was present only in a 2 cm radius from the center. In the No VF version feedback was present only for distances longer than that of the target.

108 sensory stimulation only when the VF is not present. These findings have major implications for evaluating
109 the use of sub-sensory electrical stimulation during the execution of complex tasks.

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111 **2. Methods.**

112 **2.1 Participants**

113 A total of 40 healthy individuals (19 females, age 24.0 ± 4.3 years) volunteered for this study by signing an
114 informed consent. All the experimental procedures were approved by the Ethical Committee of University
115 College Dublin and have been conducted according to the WMA's declaration of Helsinki. No personal or
116 sensitive data were collected for the study. This consisted of four different experiments executed using the
117 same experimental setup. Each subject participated to two of the experiments twice (one common to all
118 subjects and one group-specific) during two experimental sessions performed in different days, often within
119 the same week.

120 **2.2 Experimental Setup**

121 During all experiments, subjects sat on a chair placed in front of a computer screen placed at a distance of
122 1 m (**Fig. 1**). The elevation of the chair was controlled so to keep the shoulder abducted at 100° . Subjects
123 had the right hand strapped to a manipulandum attached to a tri-axial load-cell (3A120, Interface, UK),
124 while the wrist and the forearm were wrapped to the support plan and immobilized using self-adhesive tape.
125 The elbow and shoulder flexion were fixed at 90° and 60° , respectively. All experiments consisted in the
126 exertion of isometric forces against the manipulandum, as instructed by a virtual scene presented on the
127 screen. The virtual scene consisted of a grey cursor, commanded in real time by the x and y components of
128 the force exerted on the manipulandum, a filled circle indicating the center of the exercise space (0 N of
129 force applied) and a target, represented by a hollow circle. The center and target circles had a radius of 0.7
130 cm or 1.2 cm, depending on the experiment (see 2.3 and 2.4). Targets were always placed at a distance from
131 the center equal to 7.5 cm on the screen, equivalent to 12 N force exerted in the direction of the target. Data

132 from the load-cell were sampled at 50 Hz. All the software constituting the virtual scene was custom
133 developed in Labview.

134 **2.3 Sensory Threshold Selection**

135 At the beginning of each experimental session for each subject, a procedure for the identification of the
136 subject- and session-specific sensory threshold (ST) was performed. Two electrodes for electrical
137 stimulation (5x5 cm, Valutrode Lite, Axelgaard, US) were positioned on the lateral head of the triceps
138 brachii (TLH) muscle. This muscle was chosen as in this type of setup has proven to be the muscle majorly
139 involved in reaching the upper right part of the workspace (De Marchis et al., 2018). The electrodes were
140 placed at about 2/3 the length of the muscle belly in each direction. The ST was defined as the smallest
141 noise-stimulation current (white Gaussian noise, bandwidth 0.1-1000 Hz) that the subject could perceive
142 and was calculated by iteratively increasing the root mean square value (RMS) of the stimulation noise by
143 10 μ A (starting from 0) every 30 seconds until the subject started feeling a clear tingling sensation under
144 the electrodes. Stimulation was administered using a voltage-driven current stimulator (Model 2200, A-M
145 Systems, US), commanded using a custom software developed in Labview. The ST level was estimated for
146 each subject during each experimental session.

147 **2.4 Optimal stimulation experiment.** The study consisted of four different experiments all executed using
148 the setup just described. The experiments consisted of an optimal stimulation (OS) experiment (to which
149 all subjects participated twice) and in three different versions of a visuomotor adaptation (VMA)
150 experiment (of which each subject experienced only one version, twice), each version characterized by a
151 different VF on the cursor trajectory presented during the task performance.

152 The aim of the OS experiment was to determine the session-specific optimal stimulation level for each
153 subject, defined as the level of sub-sensory stimulation that maximizes performance by decreasing task
154 variability in the absence of VF. During the OS experiment subjects performed a series of reach-and-hold
155 tasks, consisting of reaching for a target of 0.7 of diameter positioned in the upper right side of the screen

156 (Fig. 1) and of holding the cursor as close as possible to the center of the target for 30 seconds. The VF was
157 projected on the screen only during the reaching phase and for the first 10 s after they reached the target,
158 and was then removed. During each task, subjects received sub-sensory noise stimulation on their TLH
159 muscle at six different current levels, equal to 0% (no current), 50%, 60%, 70%, 80% or 90% of their ST.
160 Subjects experienced each level of sub-sensory stimulation five times in a random order, for a total of 30
161 repetitions (6 current levels x 5 times). The session-specific OS level was estimated at the end of each OS
162 experiment as the percentage of ST (excluding 0% ST) yielding the smallest average (across the 5
163 repetitions for each percentage) standard deviation in the Cartesian distance between the cursor and the
164 target during the 20 s of the hold phase of the task where the visual feedback was not present (*stdDist*).
165 Additional analyses were performed in post processing. Specifically, we checked for statistically significant
166 differences (Wilcoxon's signed rank test, $\alpha=0.05$) in the average *stdDist* between OS and 0% ST across all
167 subjects. We then analyzed the distribution of the OS percentages across the different stimulation levels,
168 for both OS experiments of all subjects. Finally, we analyzed the relationship between the stimulating
169 current and the motor performance by fitting a first order polynomial, using a least square algorithm on the
170 average *stdDist* values relative to each stimulation intensity. The quality and significance of the fitting was
171 evaluated by calculating Pearson's coefficient ρ .

172 **2.4 Visuomotor adaptation experiment.** All three versions of the VMA experiment consisted of isometric
173 reaching movements where the subjects were asked to drive the cursor towards a random target (diameter
174 1.2 cm) presented at 7.5 cm (12 N) from the center. Subjects performed their assigned version of the VMA
175 experiment immediately after the OS one, in both sessions.

176 The versions of the VMA experiment differed only in the VF that was provided to the subject during the
177 reaching tasks. 20 subjects (9 females) performed the VMA experiment with continuous view of the
178 movements of the cursor they were driving (*Full VF*). 10 subjects (2 females) performed the VMA
179 experiment while receiving VF of the movement of the target only up to 2 cm (3.3 N) from the center of
180 the virtual scene (*Limited VF*). Finally, 10 subjects (8 females) performed the experiment with no VF (*No*

181 VF) on the movement of the cursor during the trajectory. In the *No VF* experiment subjects were shown the
182 cursor only between 0 and 0.5 cm (0.7 N) from the center and after exceeding the distance to the center of
183 the target (7.5 cm, 12 N). Thus, in the *No VF* experiment subject received feedback only on the result of
184 their reaching trial.

185 The VMA experiment consisted of 9 blocks during which the VF condition was applied. In the first 3 blocks
186 (baseline, BL1-BL3) participants were asked to reach to 8 targets positioned in a compass-like configuration
187 for 5 times in a random order (Figure 1). During these and subsequent blocks they were instructed to reach
188 for the targets as fast as possible and they were given positive feedback (consisting in the target becoming
189 green) if they were able to reach for the target in less than 1.5 seconds, and negative feedback (consisting
190 in the target becoming red) otherwise. The feedback on the speed of the trial indicated by the change in
191 color of the target was present in all three VF conditions. The targets for which a subject received negative
192 feedback were appended and repeated at the end of the block, thus making each block consisting of 40
193 movements plus the repetition of all the negative-feedback movements. After the BL blocks, subjects
194 performed three adaptation blocks (AD1-AD3) where they were asked to reach for the targets while
195 adapting to a 45° clockwise rotation applied to the mapping between the force sensor and the virtual scene.
196 The only instruction that the subjects were given was to try to obtain positive feedbacks on their movements.
197 Also in this case, subjects performed 5 repetitions of all 8 targets in a randomized order (40 tasks), and
198 repeated the targets for which they received negative feedback at the end of the trial. Finally, subjects
199 performed three unperturbed post-adaptation blocks (PA1-PA3) that were used to washout the adapted
200 motor plan. Subjects performing the *Limited VF* and *No VF* VMA versions also experienced 3 additional
201 blocks before the BL ones, that consisted of unperturbed baseline blocks with full VF (BL-VF). The aim of
202 these blocks was to allow the subjects to practice and fully understand the task before the limitation to the
203 VF was applied. Subjects performed their assigned VMA experiment in both experimental sessions, once
204 while receiving sub-sensory stimulation (through all the 9 blocks of the experiment) at the OS level
205 calculated in that same experimental session (*Stim*), and once without stimulation (*NoStim*), in a random

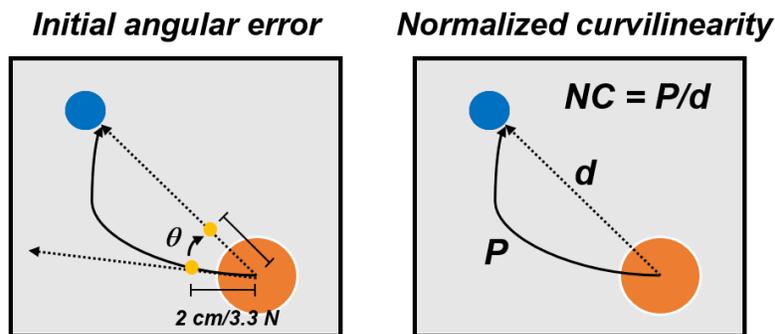


Figure 2. Performance metrics for the VMA experiment. The initial angular error (left) was calculated, for each movement repetition, as the angle between the actual and optima trajectories at 2 cm from the center of the workspace. The normalized curvilinearity (right) was calculated, for each movement repetition, as the ratio between the actual movement path and the ideal one.

206 order. The stimulation level used during the *Stim* condition was the one identified for the subject during the
207 OS experiment of that specific session. Participants were blinded to the condition. For all three versions of
208 the VMA experiment, half of the assigned subjects performed the *Stim* condition in the first experiment,
209 the other half in the second experiment. For each reaching repetition, we analyzed the center-out portion of
210 the movement, from the moment in which the cursor exited the origin target to the moment it reached the
211 goal target. Each center-out movement was extracted and length-normalized over 100 data points. We
212 analyzed the trajectory data by means of two metrics (**Fig. 2**): the initial angular error (IAE) and the
213 normalized curvilinearity (NC). The IAE was calculated as the angle between the straight line connecting
214 the ideal path and the actual path of the movement at 2 cm from the origin. This distance was selected
215 because subjects performing the *Limited VF* experiment had the VF removed after 2 cm, thus for them this
216 metric represents the angular error before losing VF. The NC was defined as the ratio between the actual
217 distance covered by the cursor between the center and the target and the length of the straight line
218 connecting the center and the target. The IAE is intended to capture the error in movement planning before
219 the onset of potential compensations, while the NC metric accounts for both the initial movement error and
220 the changes in motor plan that the subject undergoes to compensate for the shooting error. The analysis of
221 IAE and NC was performed on the first 40 movements of each block (thus excluding the repeated trials in

222 each blocks) and the behavior of the two metrics was analyzed both movement-by-movement and as
223 average in each block. Moreover, the analysis were differentially performed on all targets together and by
224 considering only the targets were the triceps are active (that are, using a compass notation, targets N, NE
225 and E, as estimated in (De Marchis et al., 2018) using the same experimental setup) or the targets were the
226 triceps are not involved (all targets excluding N, NE and E).

227 Finally, for all three versions of the VMA experiment, we compared the number of repeated trials (thus the
228 number of errors) across subjects in the first block of adaptation (AD1) between the *Stim* and *NoStim*
229 conditions. This comparison was based on a Wilcoxon's signed rank test with significance level $\alpha = 0.05$.

230 **3. Results**

231 **3.1 OS Experiment.** The results of the OS experiments performed by the subjects in the two experimental
232 sessions were pooled together in the analysis. Thus, the 80 instances (40 subjects x 2 experimental sessions)
233 were treated as independent measures. As expected from similar experiments (Magalhaes and Kohn, 2012;
234 2014; Severini and Delahunt, 2018), we consistently observed a decrease in accuracy during the hold-phase
235 of the OS task when the VF was removed (example for one trial of one subject in **Fig. 3A**). From the
236 analysis of the OS levels, considering also the trials where no current was actually applied (0%), we
237 observed that in 7 instances out of 80, the average *stdDist* was lower for 0% stimulation than for a
238 stimulation level above 0%. This accounts for 8.75% of the instances, against a value expected by chance
239 of 13.33% (**Fig. 3B**). For the instances in which the 0% level presented the lowest average value of *stdDist*
240 across the task repetitions, the value of OS was selected as the value of actual stimulation (thus above 0%)
241 which yielded the lowest average *stdDist* (**Fig. 3B**). The OS levels were mostly distributed towards
242 percentages close to the ST (**Fig. 3B**) with 59 out of 80 OS levels observed for percentages of ST above
243 70%. We observed statistically significant lower values of *stdDist* for OS with respect to 0% stimulation
244 ($p < 0.01$ using Wilcoxon's signed rank test), also considering the instances were 0% yielded the average
245 lower *stdDist* results (**Fig. 3C**). Finally, we analyzed the correlation between the RMS of the stimulation
246 current and the *stdDist* metric.

247 We observed a negative correlation (**Fig. 3D**) between the average *stdDist* metric (averaged across all
248 repetitions associated with a specific current level across subjects) and the relative RMS values of
249 stimulation current, characterized by a significant ($p < 0.001$) linear fitting with $\rho = -0.64$. This fitting
250 indicates that, in our dataset, the performance increases with the RMS of the stimulation.

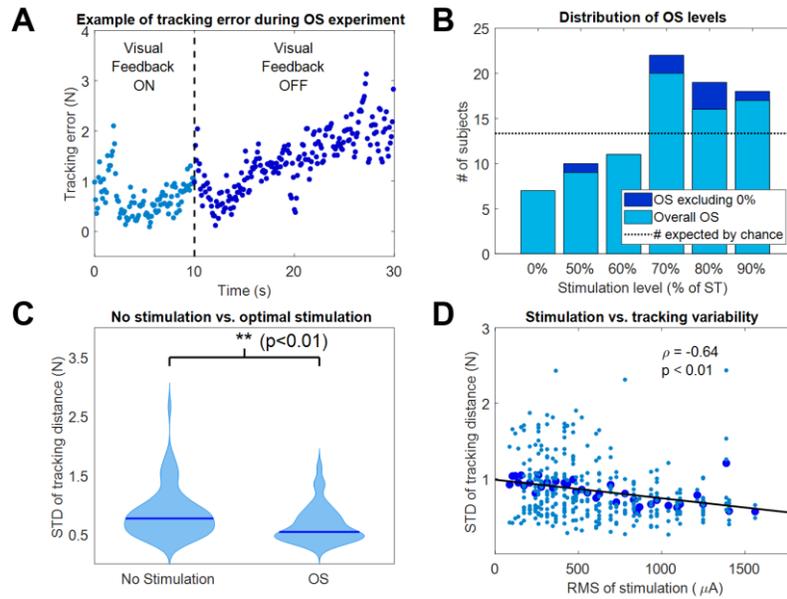


Figure 3. Results of the OS experiment. (A) Example of tracking error during a representative instance of the OS experiment. Movement variability around the target position increased as visual feedback was removed. (B) Distribution of the OS values, both including (light blue) and excluding (dark blue) the 0% level. (C) Violin plots of the tracking variability between OS values and 0% (no stimulation) values. ** indicates significant differences (Wilcoxon's signed rank test) with $p < 0.01$. (D) Correlation between the RMS of stimulation and the STD of the tracking distance during the OS experiment.

251 3.2 VMA Experiments.

252 The results for the *Full VF* version of the VMA experiment (**Figure 4**) were in line with what had been
 253 observed in literature (Shadmehr and Mussa-Ivaldi, 1994) (**Fig. 4A**). Subjects presented marked movement
 254 errors, reflected in both the IAE and NC metrics, in the first block of perturbation (AD1) that were
 255 compensated over time. After-effects opposite to the direction of the original perturbation (in the IED) were

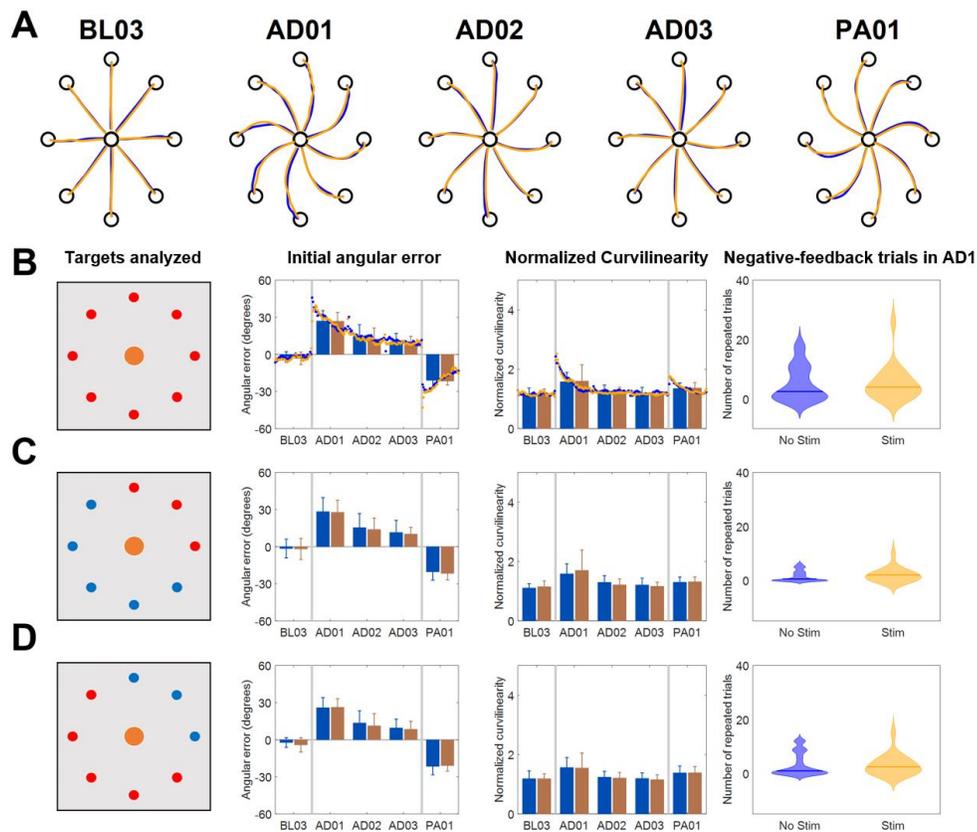


Figure 4. Results of the VMA *Full VF* experiment. (A) Example of force traces to targets for representatives blocks of the experiment. (B) Average, across subjects, performance metrics. The first panel from the left presents the targets analyzed (in red). The second panel presents the initial angular error metric, both as mean \pm standard deviation across the first 40 trials of each block (bars and whiskers) and as average (across subject) of the metric extracted for each single reaching movement for the first 40 trials (dots). The third panel presents the normalized curvilinearity metric, in the same notation. The fourth panel presents the violin plots of the number of negative-feedback trials (that had to be repeated) during AD1. (C) and (D) present the same results for only the upper right quadrant targets of the workspace (where the muscles stimulated are active) and for the remaining targets. In this case the metric plots are presented only as the mean \pm standard deviation across the trials of those targets in each block. In all plots, blue indicates the *NoStim* condition, Orange the *Stim* condition.

256 present at the beginning of the post-adaptation phase and quickly vanished by the end of the experiment.
 257 When comparing the *Stim* and *NoStim* conditions, we were not able to observe substantial differences in
 258 trends in both metrics, such as a faster/slower adaptation speed or different values of IED or NC at the
 259 beginning of AD1 or at the end of AD3. This would have indicated, a higher/lower initial error and a
 260 higher/lower level of compensation of the error, respectively. Instead, both conditions presented remarkably
 261 similar trends in both metrics when considering all targets (**Fig. 4B**), only the targets where the triceps are

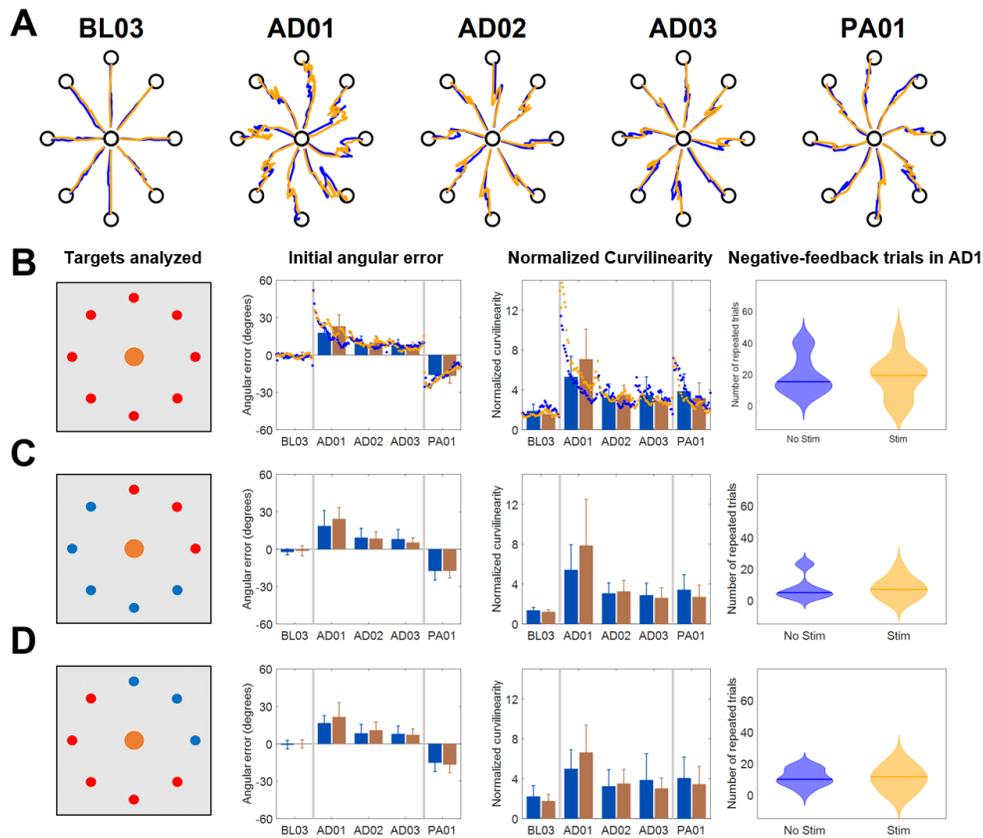


Figure 5. Results of the VMA Limited VF experiment. (A) Example of force traces to targets for representatives blocks of the experiment. (B) Average, across subjects, performance metrics. The first panel from the left presents the targets analyzed (in red). The second panel presents the initial angular error metric, both as mean \pm standard deviation across the first 40 trials of each block (bars and whiskers) and as average (across subject) of the metric extracted for each single reaching movement for the first 40 trials (dots). The third panel presents the normalized curvilinearity metric, in the same notation. The fourth panel presents the violin plots of the number of negative-feedback trials (that had to be repeated) during AD1. (C) and (D) present the same results for only the upper right quadrant targets of the workspace (where the muscles stimulated are active) and for the remaining targets. In this case the metric plots are presented only as the mean \pm standard deviation across the trials of those targets in each block. In all plots, blue indicates the *NoStim* condition, Orange the *Stim* condition.

262 active (**Fig. 4C**) and the targets where the triceps were not active (**Fig. 4D**). Similarly, we did not observe
263 significant differences in the number of errors made by the subjects in AD1 between the two stimulation
264 conditions for all the target groupings (rightmost panel, **Fig. 4B, 4C** and **4D**).

265 In the *Limited VF* version of the VMA experiment (**Figure 5**), trajectories were characterized by initial
266 shooting errors followed by abrupt deviations once the VF was removed (**Fig. 5A**). As the AD blocks
267 progressed, subject showed decreased shooting errors (also captured by a progressive decrease in IAE and
268 NC) but still exhibited abrupt modifications in their trajectories once the feedback was removed. When
269 comparing the *Stim* and *NoStim* conditions we observed a qualitative trend where *Stim* trials were
270 characterized by higher initial values of IAE and NC at AD1 with respect to *NoStim*. The two conditions
271 exhibited similar values on both metrics at AD3. The trends observed appeared to be present on all targets,
272 regardless of groupings (**Fig. 5B, 5C** and **5D**). Finally, we did not observe significant difference in the
273 number of errors at AD1 between the two conditions.

274 In the *No VF* version of the VMA experiment (**Figure 6**), once again we observed initial changes in both
275 metrics at AD1 due to the rotation. These changes were compensated over the trials even without VF
276 (consistently with what shown in Scheidt et al., 2005) although to a smaller level with respect to the *Full*
277 *VF* experiment (**Fig 6A** and **4A**). Also in this case, the adaptation behaviors were reflected in both metrics.
278 We did not observe differences in the behavior of the IAE and NC metrics between the two stimulation
279 conditions, either for all the targets or for the different groupings. However, the *NoStim* condition presented
280 a significant higher number of reaching errors at AD1 with respect to the *Stim* condition that was observed
281 for all the targets together ($p = 0.046$, **Fig. 6B**) and for the grouping representing only the targets where the
282 triceps were active ($p = 0.043$, **Fig. 6C**).

283 **4. Discussion**

284 In our results we observed that sub-sensory electrical stimulation was associated with smaller
285 movement variability during the phase of the OS experiment where VF was not available and task

286 performance depended solely on proprioceptive feedback. Moreover, we observed a correlation between
287 stimulation current and movement variability whereas higher current levels were associated with better task
288 performance across subjects. These results, taken together, further confirm that sub-sensory electrical
289 stimulation can improve task performance in tasks where proprioception is the primary feedback modality
290 (Gravelle et al., 2002; Ross and Guskiewicz, 2006; Collins et al., 2014; Severini and Delahunt, 2018).

291 On the other hand, we observed only small evidence of an effect of the stimulation during the VMA
292 experiments, that was mainly characterized by a significant decrease in negative-feedback movements (that
293 are movements that took more than 1.5 seconds for the subject to complete) between the two stimulation
294 conditions during the first block of adaptation for the subjects that performed the *No VF* version of the
295 experiment. When the VF of the trajectory was present, completely or partially, we did not observe
296 substantial differences in task performance, as captured by two different metrics, between the *Stim* and
297 *NoStim* conditions other than a qualitative slight decrease in task performance during AD1 for the *Limited*
298 *VF* group. In the following, we will further discuss upon these results.

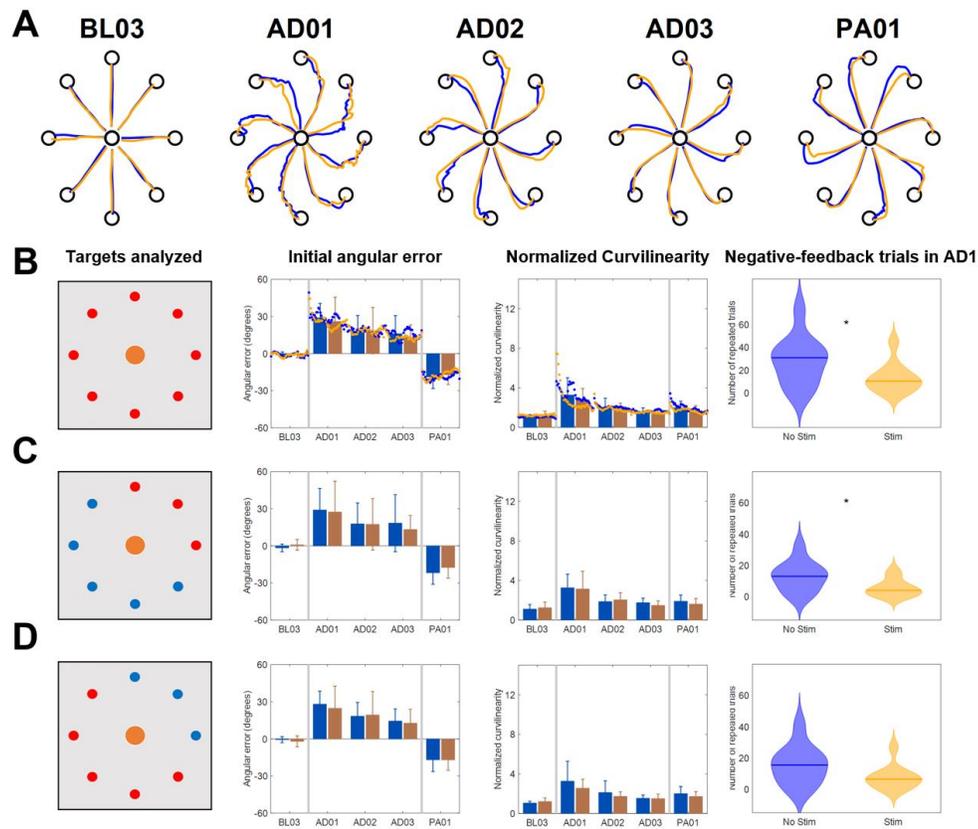


Figure 6. Results of the VMA *No VF* experiment. (A) Example of force traces to targets for representatives blocks of the experiment. (B) Average, across subjects, performance metrics. The first panel from the left presents the targets analyzed (in red). The second panel presents the initial angular error metric, both as mean \pm standard deviation across the first 40 trials of each block (bars and whiskers) and as average (across subject) of the metric extracted for each single reaching movement for the first 40 trials (dots). The third panel presents the normalized curvilinearity metric, in the same notation. The fourth panel presents the violin plots of the number of negative-feedback trials (that had to be repeated) during AD1. * indicates significant differences (Wilcoxon’s signed rank test) in the number of negative-feedback trials with $p < 0.05$ ($p = 0.046$ in (B) and $p = 0.043$ in (C)). (C) and (D) present the same results for only the upper right quadrant targets of the workspace (where the muscles stimulated are active) and for the remaining targets. In this case the metric plots are presented only as the mean \pm standard deviation across the trials of those targets in each block. In all plots, blue indicates the *NoStim* condition, Orange the *Stim* condition.

299 The results of the OS experiment provide, in this study, the strongest evidence of the effectiveness
 300 of sub-sensory stimulation in boosting proprioception and influence task performance. In the OS
 301 experiment we did not observe a clear SR behavior, characterized by a U-shaped relationship between the
 302 change in performance and the intensity of the stimulation (Collins et al., 1995). Such behavior is unlikely
 303 to appear in a group analysis (Bates, 1996; Severini and Delahunt, 2018), given the differences in ST across

304 subjects and across different sessions for the same subjects that have been observed in this and previous
305 studies (Magalhaes and Kohn, 2012; 2014). Nevertheless, we did observe a significant negative correlation
306 between the stimulation intensity and the tracking error (**Fig. 3D**), suggesting that sub-sensory stimulation
307 is more effective as its intensity increases. This linear relationship does not rule out the presence of a SR-
308 like behavior, but hints that such behavior may arise by considering stimulation intensities that are above
309 the ST of subjects. On the other hand, stimulating currents above ST could lead to additional confounding
310 factors affecting motor task performance related to the increase in attention or arousal, and the few studies
311 that investigated the use of supra-sensory stimulation levels in humans found that it leads to an overall
312 decrease in performance (Iliopoulos et al., 2014; Severini and Delahunt, 2018). The results of the OS
313 experiment support the design choice of using sub-sensory stimulation levels close but below ST
314 (frequently 90% of ST) that is often employed in similar studies (Gravelle et al., 2002; Magalhaes and
315 Kohn, 2012; 2014).

316 In contrast with the results obtained in the OS experiment, we observed little evidence of an effect
317 of the stimulation during the different VMA experiments. In the *Full VF* version of the experiment, the
318 adaptation patterns were remarkably similar between the two stimulation conditions. We observed some
319 small differences in performance between the two stimulation conditions in the first block of adaptation for
320 both the *Limited VF* and the *No VF* versions of the experiment, although results appear to be more solid in
321 the latter rather than the former. In the *Limited VF* experiment we qualitatively observed higher values in
322 both performance metrics during AD1 for the *Stim* condition. In the *No VF* experiment we did not observe
323 differences in trends between the two metrics, but the *Stim* condition was characterized by a significant
324 smaller number of negative-feedback trials, especially for the targets of the upper right quadrant, where the
325 muscle undergoing stimulation was active. Both the trends that we observed in the *Limited VF* and *No VF*
326 experiments could be potentially explained by the stimulation impacting the weighting process between
327 proprioceptive and visual feedbacks that happens during reaching tasks in general, and motor adaptations
328 in particular. Previous studies have shown that different feedback modalities mix flexibly during the

329 execution of voluntary movements and during motor adaptations (Sober and Sabes, 2003; Scheidt et al.,
330 2005; Sober and Sabes, 2005; Shabbott and Sainburg, 2010). While visual feedback is responsible for
331 estimating the limb position required in the planning of the movement trajectory, proprioception contributes
332 in generating the necessary feedforward commands required for movement execution (van Beers et al.,
333 2002; Sober and Sabes, 2003; 2005). Primary and secondary muscle spindles have been observed to
334 increase their firing rates during isometric contractions (Edin and Vallbo, 1990), indicating that these
335 afferents encode information on muscular state even if the muscles are not changing in length. A previous
336 study on spindles behavior during visuomotor adaptations has shown that adaptation leads to a progressive
337 decrease in the activity of the spindles (Jones et al., 2001). The authors linked this result to the fact that
338 adaptation to visuomotor rotations is achieved by updating the internal models mapping the kinematics of
339 the movement, a process relying mostly on visual and less on proprioceptive feedback (Krakauer et al.,
340 1999; Krakauer, 2009), as confirmed also in a study involving individuals with proprioceptive deficits
341 (Lajoie et al., 1992). Decreasing the weight of the spindles' information during visuomotor adaptation
342 would then help resolving the conflict between the visual and proprioceptive maps that the perturbation
343 induces (Jones et al., 2001). This re-weighting of proprioceptive information has been shown to happen
344 centrally, at the level of the somatosensory cortex, rather than at the spinal level (Bernier et al., 2009), and
345 to be more prominent at the beginning of the adaptation period and then alleviated as the adaptation
346 converges.

347 Thus, as the activity of the spindles is down-regulated at the beginning of adaptation, the supposed
348 enhancement of such activity by the stimulation would effectively clash with the sensory re-weighting
349 process. This clash, in the *Limited VF* experiment, where VF of the shooting error is provided but
350 proprioceptive feedback is still necessary for successfully completing the task, could translate in bigger
351 initial errors as the stimulation supposedly antagonizes the spindle down-regulation. The fact that a similar
352 effect is not present if the *Full VF* experiment could be explained by the primacy of VF over proprioception
353 during visuomotor adaptations that bypasses the potential effects of the stimulation. On the other hand, in

354 the *No VF* experiment, where proprioception is the only available feedback modality, its supposed boost
355 through the stimulation may lead to increased feedback reliability that may translate in a smaller number
356 of negative-feedback trials.

357 These explanations, although plausible, cannot be fully confirmed from these results due to the
358 small sample examined in the experiments from which they have been derived, that must be listed as main
359 limitation for the study herein presented. Another potential limitation of this study, that could also help
360 explain the differences in stimulation effectiveness that we observed between the OS and VMA
361 experiments, could be represented by the fact that we selected the optimal stimulation level based on the
362 performance during the holding phase of the OS experiment and then tested it during a reaching task in the
363 VMA experiments. In a literature review recently published by Shadmehr (Shadmehr, 2017) the author
364 raised the possibility that these two tasks (holding and reaching), similarly to what happens during ocular
365 movements, employ different neural circuitries. In this interpretation, the discrepancy in stimulation
366 effectiveness that we observe could be explained by an experimental design flaw where we used optimal
367 currents derived from the holding task in a task that employs different neural circuits. Nevertheless,
368 although there is evidence on the different nature of neural inputs during reaching and holding, no
369 information is available on if and how proprioceptive feedback is processed differently between these two
370 tasks.

371 To summarise, the results presented in this study further support the hypothesis that sub-sensory
372 currents applied to the surface of the muscles affect proprioceptive feedback during movement, but this
373 effect appears to be clearly beneficial for task performance only in tasks where proprioception is the primary
374 feedback modality.

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