

1 **Passive sensorimotor stimulation triggers long lasting alpha-band fluctuations in visual**  
2 **perception**

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15 **Running head:** the sensorimotor system synchronizes vision

16 **Key words:** sensorimotor, oscillations, active sensing, alpha, visual perception

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26 **Abstract**

27 Movement planning and execution rely on the anticipation and online control of the incoming  
28 sensory input. Evidence suggests that sensorimotor processes may synchronize visual rhythmic  
29 activity in preparation of action performance. Indeed, we recently reported periodic  
30 fluctuations of visual contrast sensitivity which are time-locked to the onset of an intended  
31 movement of the arm. However, the origin of the observed visual modulations has so far  
32 remained unclear due to the endogenous (and thus temporally undetermined) activation of the  
33 sensorimotor system that is associated with voluntary movement initiation. Here, we activated  
34 the sensorimotor circuitry involved in the hand control in an exogenous and controlled way by  
35 means of peripheral stimulation of the median nerve and characterized the spectrotemporal  
36 dynamics of the ensuing visual perception. The stimulation of the median nerve triggers robust  
37 and long-lasting (~1 s) alpha-band oscillations in visual perception, whose strength is  
38 temporally modulated in a way that is~~temporal evolution resembles that of~~ consistent with the  
39 changes in ~~well-described~~ alpha power described at the neurophysiological level ~~modulations~~  
40 ~~induced by~~ after sensorimotor stimulation. These findings provide evidence in support of a  
41 causal role of the sensorimotor system in modulating oscillatory activity in visual areas with  
42 consequences for visual perception.

43

44 **New & Noteworthy**

45 This study shows that the peripheral activation of the somatomotor hand system triggers long-  
46 lasting alpha periodicity in visual perception. This demonstrates that, not only the endogenous  
47 sensorimotor processes involved in movement preparation, but also the passive stimulation of  
48 the sensorimotor system can synchronize visual activity. The present work suggests that  
49 oscillation-based mechanisms may sub-serve core (task-independent) sensorimotor integration  
50 functions.

51

## 52 **Introduction**

53 Any motor act entails a coordinated pattern of muscle contractions and the anticipation  
54 and online monitoring of the sensory effects associated with it. Proprioceptive and tactile  
55 afferences, in particular, carry critical information for the planning of movement. Some  
56 theories posit that motor planning actually consists in determining the appropriate motor  
57 commands to achieve a certain somatosensory goal (Lemon, 2008). Indeed, the somatosensory  
58 function is an integral part of the brain machinery involved in motor activity. Besides involving  
59 a prediction of the ensuing somatosensory state, motor programming is also accompanied by  
60 preparatory changes in visual function (Gutteling et al., 2011; Rolfs et al., 2013; Tomassini and  
61 Morrone, 2016). Interestingly, we recently reported periodic ~~theta band~~ fluctuations of visual  
62 contrast sensitivity which are time-locked to the onset of an intended movement of the arm  
63 (Tomassini et al., 2015). A follow-up EEG study revealed that a theta-band (~4 Hz) brain  
64 rhythm observed during motor preparation not only predicts visual performance on a trial-by-  
65 trial basis, but also aligns to the upcoming hand movement (Tomassini et al., 2017),  
66 representing the likely neurophysiological underpinning of the previously reported behavioral  
67 modulations. ~~This This phenomenon phenomenon~~ does not require specific visuo-motor  
68 contingencies, as it occurs for visual stimuli that are unrelated to the motor task (Benedetto et  
69 al., 2016; Tomassini et al., 2015; Tomassini et al., 2017), and generalizes, with ~~very~~ similar  
70 behavioral featuresignatures, to the oculomotor behavior (Benedetto and Morrone, 2017;  
71 Hogendoorn, 2016; Wutz et al., 2016). Most importantly, visual oscillatory modulations  
72 already emerge during the motor planning stage, long before the movement is actually executed  
73 (Tomassini et al., 2015; Tomassini et al., 2017) ~~(Tomassini et al., 2015)~~. Altogether, these  
74 findings point to an early and automatic form of visuomotor coupling. Oscillatory mechanisms

75 may thus regulate the information flow within an extended sensory-motor network (including  
76 early visual areas), in preparation of action performance.

77 Indeed, oscillatory activity is now widely acknowledged to be a critical component of  
78 brain functioning, which directly participates in regulating effective neuronal communication  
79 and selective information routing (Buzsaki and Draguhn, 2004; Fries, 2015; Schroeder and  
80 Lakatos, 2009). Evidence suggests that the ongoing oscillatory dynamics ~~not only predicts~~  
81 explains trial-by-trial variability in perceptual performance (Ai and Ro, 2014; Busch et al.,  
82 2009; Busch and VanRullen, 2010; Mathewson et al., 2009), ~~but and also~~ flexibly adjusts  
83 according to task demands, leading to behavioral benefits (Bonnefond and Jensen, 2012; Cravo  
84 et al., 2013; Lakatos et al., 2009; Morillon et al., 2014; Samaha et al., 2015) .

85 Oscillations have also proved susceptible to a phase-reset by external stimuli (Lakatos et  
86 al., 2009; Mercier et al., 2013; Mercier et al., 2015). By exploiting the systematic phase  
87 modulation induced by sensory stimulation, a number of studies have shown periodic  
88 fluctuations in visual performance following either visual (Drewes et al., 2015; Fiebelkorn et  
89 al., 2013; Landau and Fries, 2012; Song et al., 2014) or auditory (Diederich et al., 2012;  
90 Fiebelkorn et al., 2011; Romei et al., 2012) stimulus presentation.

91 Contrary to the sensory-induced phase modulation and the associated behavioral  
92 periodicity, the movement-locked rhythmicity in visual perception does not, however, entail a  
93 univocal interpretation (see (Tomassini et al., 2015; Tomassini et al., 2017). One possibility is  
94 that the sensorimotor system is capable of exerting endogenous control over visual ~~oscillatory~~  
95 activity by, for example, resetting the phase of ongoing oscillations in visual areas.  
96 Alternatively, the probability of spontaneous movement initiation and the sensitivity of the  
97 visual system might be jointly regulated by the phase of an ongoing rhythm, which could be of  
98 ~~different-non-motor~~ origin (e.g., a central rhythm).

99           So far, this phenomenon has only been investigated in the context of voluntary action,  
100 when an intention to move is formulated, prompting the sensorimotor control processes that  
101 eventually lead to action execution. On the one hand, the lack of experimental control over the  
102 exact timing of the sensorimotor system activation highlights the endogenous nature of the  
103 observed oscillatory modulations but, on the other hand, makes it difficult to determine their  
104 origin, eluding the identification of a clear ‘resetting’ event. It is thus unknown ~~whereas~~  
105 whether similar oscillations in visual perception would still be observed upon activation of the  
106 sensorimotor system, but in the absence of those (endogenous) neural processes which are  
107 specifically engaged by spontaneous movement initiation.

108           The present study was set out to address this issue. To this aim, we exploited the electrical  
109 stimulation of the median nerve as a way to get exogenous and temporally precise access to  
110 the activation of the sensorimotor circuitry involved in the hand control. Thanks to the  
111 externally-triggered manipulation, we could probe visual performance with a high sampling  
112 rate (~30 Hz) and for a long time (> 1 s). We therefore characterized in detail the  
113 spectrotemporal dynamics of visual perception ensuing the peripheral stimulation of the  
114 somatomotor system of the hand.

115

## 116 **Methods**

### 117 *Subjects*

118           Seven subjects participated in the study (one author, A.D.; four females; age 27.8±6 SD).  
119 Excepting the author, subjects were all naïve with respect to the aims of the study and were all  
120 paid (€10/h) for their participation. All subjects were right-handed (Oldfield, 1971) and had  
121 normal or corrected-to-normal vision. The study and experimental procedures were approved  
122 by the local ethics committee (ASL 3 Genova). Participants provided written, informed consent  
123 after explanation of the task and experimental procedures, in accordance with the Declaration

124 of Helsinki and the local ethics committee.

125 *Experimental setup and procedure*

126 Participants sat in a dark room, in front of an LCD monitor (24''; 60 Hz) at a viewing  
127 distance of ~57 cm, with both their arms folded on the table and hidden from view by a  
128 cardboard. They were asked to report verbally the orientation of a Gabor with near-threshold  
129 contrast, tilted by  $\pm 45^\circ$ , and embedded within dynamic visual noise. The visual task was the  
130 same as what used by Tomassini et al., 2015 (Tomassini et al., 2015) except that the Gabor  
131 (spatial frequency, 1 c/deg; duration, 0.033 s, two frames) was presented at one central location  
132 instead of two locations ( $7.5^\circ$  below the fixation point; see Figure 1).

133 Each trial started with the display of dynamic visual noise (RMS contrast equal to 0.11;  
134 refreshed every second frame, 0.0165 s) and fixation point (black square,  $0.4 \times 0.4^\circ$ ) on screen.  
135 At variable delays between 0.5 and 1.5 s from the start of the trial, the right median nerve was  
136 stimulated. Bipolar electrical stimulation, with monophasic square wave of 100  $\mu$ s (DS7A,  
137 Digitimer Ltd., England) was delivered on the volar aspect of the wrist (Fig.1), according to  
138 standard peripheral nerve stimulation montage. The intensity of the stimulation was adjusted  
139 for each subject so that it produced a small visible twitch of the thumb. As reported by all  
140 participants, the electrical stimulation was not painful. Gabor presentation times were varied  
141 randomly on a trial-by-trial basis from 0.05 to 1.15 s after the median nerve stimulation in steps  
142 of 0.033 s (two frames). Visual performance was therefore sampled at ~30 Hz within a 1.1 s  
143 time-window following the electrical stimulation of the median nerve. In addition to probing  
144 visual performance after the stimulation of the median nerve, the Gabor could also appear at  
145 one of three randomly chosen times before the electrical pulse (-0.25, -0.15 and -0.05 s) with  
146 an overall probability of 15%.

147 A photodiode (2.3 x 2.3 cm) placed on the top left corner of the monitor was used to  
148 record the accurate timing of the visual stimulations (visual noise and Gabor). A white square

149 (2 x 2 cm) was displayed on the screen in the position of the photodiode (hidden from view) in  
150 synchrony with the onset of the visual noise (trial onset) and again with the onset of the Gabor  
151 (see snapshot in Fig.1). The photodiode signals were recorded by a National Instruments data  
152 acquisition device (sampling rate, 1000 Hz) providing the times of both trial onset and stimulus  
153 appearance. The same acquisition device was also used to record a TTL (Transistor-Transistor  
154 Logic) signal corresponding to the time when the median nerve stimulation was delivered so  
155 that all the relevant events in the trial were accurately synchronized.

156 Data were collected in separate blocks of 80 trials each. A preliminary testing phase (~30  
157 trials) allowed participants to familiarize themselves with the task and provided an indication  
158 of the individual performance levels. Stimulus contrasts were initially centered around the  
159 values yielding 75% of correct responses during the familiarization phase. Due to learning  
160 effects, the performance was monitored throughout the experiment and the Gabor contrast was  
161 adjusted in order to keep performance always near threshold. The percentage of correct  
162 responses was calculated every 20 trials in each block. The contrast was not changed if the  
163 performance was within the desired range, namely between 70 and 80%. The contrast was  
164 decreased by 0.4 dB and increased by 0.2 dB if the performance level was within 80-90% and  
165 60-70%, respectively, while it was decreased by 0.8 dB and increased by 0.4 dB if performance  
166 was  $\geq 90\%$  or  $\leq 60\%$ , respectively. The contrast of the Gabor was on average  $8.6 \pm 1\%$  (SE). To  
167 avoid excessive fatigue and frustration due to the difficulty of the visual task, we also included  
168 catch trials (every 10 trials starting from the 1<sup>st</sup> trial) in which a clearly visible Gabor was  
169 presented (Gabor contrast:  $17 \pm 1\%$ ; MEAN $\pm$ SE). Catch trials were excluded from the analysis.

170 Participants completed on average  $21.3 \pm 0.6$  (SE) blocks of trials in four separate days (2  
171 hrs. testing each day), yielding in total  $1529 \pm 97$  (MEAN $\pm$ SE) trials per subject.

#### 172 *Data analysis*

173 To evaluate statistically the spectral content of the time course of visual performance

174 after the stimulation of the median nerve we used two different analysis methods: 1. a fixed  
175 effect test based on fast Fourier transform (FFT) on the aggregated data from all participants,  
176 and 2. a random effect test based on logistic regression.

#### 177 Fixed effect analysis

178 First, we pooled the data from all participants and calculated the percentage of correct  
179 responses in the visual task for each stimulus presentation time after the median nerve  
180 stimulation (stimulus latencies in the range between 0.05 and 1.15 s in steps of 0.033 s;  
181 sampling rate 30 Hz). The resulting behavioral time series was then detrended (see below),  
182 tapered (Hanning window) and fast Fourier transformed. A nonparametric permutation test was  
183 used to evaluate the presence of periodic components in the visual performance. We generated  
184 a surrogate spectral distribution by iteratively (1000 times) randomizing stimulus presentation  
185 times. Each iteration of the randomization procedure yielded a surrogate data set that was  
186 submitted to the same analysis performed on the original data set (linear detrending, Hanning  
187 tapering and FFT), producing a distribution of power spectra (under the null hypothesis that  
188 stimulus presentation time does not affect visual performance). The power derived from the  
189 FFT output of the original behavioral time series was then compared at each frequency (from  
190 1.5 to 14.5 Hz) with the surrogate power distribution. The p-value of the permutation test is  
191 yielded by the proportion of values of the surrogate distribution exceeding the power in the  
192 original data set. The p-values were corrected for multiple comparisons across frequencies by  
193 controlling the False Discovery Rate (FDR; described in (Benjamini and Yekutieli, 2001).

194 Because we were primarily interested in identifying the periodic components in the  
195 behavioral time series, prior to the spectral analysis we applied linear detrend (method of least-  
196 squares) to remove the systematic decline in the performance level over time. We evaluated  
197 statistically the consistency of the linear trend both at the single-subject and at the group-level.  
198 Specifically, we submitted the individual behavioral time series to linear regression analysis.



219 Moreover, a paired sample t-test was used to assess whether the performance level changed  
220 between the first (0.05-0.6 s) and the second (0.6-1.15 s) half of the behavioral time course  
221 following the median nerve stimulation.

#### 222 Random effect analysis

223 ~~The group level analysis~~We performed the same random-effect analysis as previously  
224 ~~adopted by Tomassini and colleagues (2017)~~(Tomassini et al., 2017). In brief, we  
225 ~~tested~~~~consisted in testing~~ whether a sinusoidal function with consistent ~~the same~~-frequency and  
226 phase across participants ~~significantly~~ ~~significantly~~ predicts visual performance. To this aim,  
227 ~~we we first fitted logistic regression models used logistic regression analysis~~(corresponding to  
228 a generalized linear model analysis – GLM – with a logit link function and a binomial  
229 distribution). ~~For to~~ each subject's behavioral data, ~~we fitted logistic regression models~~  
230 ~~including using~~ as predictors a sine and a cosine of a given frequency in the range from 1.5 to  
231 14.5 Hz (in steps of 1 Hz). ~~The probability model behind this analysis can be written as follows:~~

232 The predictive value of the phase was quantified as the norm (Euclidean length) of the  
233 sample mean ~~of the beta coefficients~~  $(\bar{\beta}_x, \bar{\beta}_z)$ :

#### 234 Time-frequency analysis

235 To characterize the temporal dynamics of the oscillatory pattern in the visual  
236 performance after the median nerve stimulation we also performed a time-frequency analysis.

237 The behavioral time series derived by pooling the data from all participants (see Fixed  
238 effect analysis) was first detrended, zero-padded and tapered (Hanning), and then fast Fourier  
239 transformed. The FFT was applied with a frequency dependent window length equal to 5  
240 cycles. Statistical evaluation was only performed for the alpha-band component which yielded  
241 significant results in the initial analysis confined to the frequency domain (i.e., 9.5 Hz). P-  
242 values were derived by applying the same permutation-based statistical approach already

223 described (see Fixed effect analysis) and subsequently FDR-corrected for multiple  
224 comparisons across time points (in the range from 0.05 to 1.15 s in steps of 0.033 s).

225

## 226 **Results**

227 Participants judged the orientation of a near-threshold Gabor (right/left-tilted by 45°) that  
228 was briefly presented at variable times just before and after they received a weak (non-painful)  
229 and unpredictable (jittered by 1 s) electrical pulse to the median nerve (see Figure 1). To fully  
230 characterize the spectrotemporal dynamics of visual perception following the stimulation of  
231 the median nerve, we probed performance with high temporal resolution (~30 Hz) and within  
232 a long time window (1.1 s).

233 Figure 2a shows the average performance in the visual orientation task (% correct) as a  
234 function of the Gabor presentation time relative to the median nerve stimulation. The  
235 behavioral time course shows an evident trend, whereby visual performance progressively  
236 declines over time. This temporal pattern is highly systematic, with all the individual time  
237 series being well described by linear functions with negative slopes (slope=-15.54±1.58;  
238 MEAN±SE; Figure 2b, top). In particular, visual performance remains above threshold level  
239 for about 0.6 s after the median nerve stimulation and drops below threshold afterwards  
240 ( $t_6=11.77$ ,  $p<0.0001$ ; paired sample two-tailed t-test; Figure 2b, bottom). No systematic change  
241 in performance is observed, instead, in the short time window preceding the median nerve  
242 stimulation ( $F_{2,12}=1.598$ ,  $p=0.242$ ; one-way ANOVA for repeated measures with time [-0.25 -  
243 0.15 -0.05 s] as within-subject factor), where performance only slightly (and non-significantly)  
244 exceeds threshold level just before the electrical pulse (i.e., at -0.05 s).

245 Interestingly, aside from the slowly developing trend, visual performance also displays  
246 faster fluctuations which seem to ensue periodically. To identify possible oscillatory  
247 components in the time-course of visual performance, we first removed the systematic linear

248 trend, and then analyzed the spectral content by applying the fast Fourier transform. Figure 3  
249 shows the detrended visual performance pooled across subjects (left panel) and its power  
250 spectrum for frequencies ranging from 1.5 to 14.5 Hz (right panel). Remarkably, a sharp peak  
251 in the power spectrum is observed at ~9.5 Hz, which is statistically significant when compared  
252 with a reference power distribution obtained by iteratively shuffling stimulus presentation  
253 times (FDR-corrected for multiple comparisons across frequencies; see Methods). This result  
254 strongly suggests that the stimulation of the median nerve triggered rhythmic fluctuations of  
255 visual performance in the alpha-band.

256 To characterize the spectrotemporal features of the perceptual time course and, in  
257 particular, to determine the extension and evolution of the oscillatory pattern, we performed a  
258 time-frequency analysis (window length, 5 cycles). The temporally-resolved power  
259 representations reported in Figure 4 reveal a long-lasting and spectrally confined oscillatory  
260 alpha-band component which emerges just after the median nerve stimulation and lasts for  
261 about 1 s. Curiously, the temporal profile of the alpha-band oscillatory power shows two  
262 distinct peaks: a brief initial enhancement after the electrical pulse (from ~0.05 to 0.25 s), is  
263 followed by a reduction in strength and then by a substantial increase in the second half of the  
264 time course, whereby it reaches its maximum value at ~0.8 s and rapidly declines thereafter.  
265 The temporal evolution of the strength of the oscillatory power/visual oscillations at 9.5 Hz is  
266 illustrated in detail in Figure 4 (right graph), showing two separate time windows with  
267 statistically significant values at the beginning and towards the final part of the time course  
268 (FDR-corrected for multiple comparisons across time points).

269 Finally, to ascertain the robustness of the identified oscillatory phenomenon and exclude  
270 the possibility that it was driven by only a minority of the subjects, we also performed an  
271 analysis at the group level. This analysis is based on logistic regression: for each subject, we  
272 first fitted models including as predictors a sine and a cosine of a given frequency in the range

273 from 1.5 to 14.5 Hz. We then used the participant-specific logistic regression coefficients (first  
274 level observations) as input for a second-level analysis in which we tested the average  
275 regression coefficient pair (sine, cosine) against zero (see Methods [and Tomassini et al., 2017](#)  
276 [for details](#)). In practice, this corresponds to testing whether a sinusoidal function with the same  
277 frequency and phase across subjects significantly predicts the perceptual performance. The  
278 results show that the perceptual time series is primarily described by two frequency  
279 components ( $p < 0.05$ , FDR-corrected for multiple comparisons across frequencies): a low-  
280 frequency component at 1.5 Hz, reflecting the slow trend, and a higher-frequency component  
281 peaking at 10.5 Hz. This analysis corroborates the presence of strong alpha-band oscillations  
282 in the visual performance time-locked to the median nerve stimulation, which are not only  
283 frequency-selective, but also phase-consistent across subjects (see Figure 5).

284

## 285 **Discussion**

286 The present study demonstrates that stimulation of the median nerve, which is intended  
287 to activate the hand somatomotor system, triggers periodic fluctuations in visual sensitivity.  
288 The rhythmicity in visual perception is spectrally confined to the alpha-band and persists for a  
289 very long time, up to nearly 1 s after the peripheral electrical pulse.

290 [Differently from a recently published study which assessed the \(within-system\) influence](#)  
291 [of the electrotactile stimulation of the finger on subsequent somatosensory perception](#)  
292 (Baumgarten et al., 2017), [the present study investigated for the first time the \(cross-system\)](#)  
293 [influence of the sensorimotor activation on low-level visual functions.](#)

294 Two features characterize the [observed](#) time course of visual performance – the fast,  
295 periodic component, and a slow worsening trend. Indeed, performance level is higher at short  
296 times following the nerve stimulation (~0.6 s), and significantly declines thereafter. This  
297 temporal trend is highly consistent across participants [and points to a possible attentional](#)

298 ~~modulation and likely of attentional origin. However, both endogenous and exogenous attention seem unlikely to account for~~  
299 ~~the present findings. First, the electrical pulse to the nerve (as well as the Gabor) was~~  
300 ~~unpredictable in time (due to the temporal jitter of 1 s), thus preventing any preparatory~~  
301 ~~deployment of attention that could be precisely locked in time to the trigger event (or to the~~  
302 ~~visual stimulus). This rules out that endogenous temporal attention may explain the initial~~  
303 ~~improvement in performance (or the periodic fluctuations) by prompting, for example,~~  
304 ~~anticipatory modulations of oscillatory activity (including phase adjustments) as shown in~~  
305 ~~previous studies for predictable stimuli (e.g., (Cravo et al., 2013; Lakatos et al., 2008;~~  
306 ~~Rohenkohl and Nobre, 2011). Moreover, the fact that a significant proportion of the Gabor~~  
307 ~~stimuli (15 %) preceded rather than followed the median nerve stimulation together with their~~  
308 ~~large temporal variability (Gabor presentation times were equally distributed over more than 1~~  
309 ~~s), avoided that the nerve stimulation provided a reliable temporal marker or a predictive cue~~  
310 ~~for the time of the Gabor appearance, further discounting the possible role of temporal~~  
311 ~~predictability and expectation. Secondly, if the stimulation of the right hand automatically~~  
312 ~~captured (exogenous) attention, diverting it from the visual stimulus location, a detrimental~~  
313 ~~rather than a beneficial effect on visual performance would be expected. Thus, stimulus-~~  
314 ~~triggered reflexive orienting of attention is also not probably the mechanism that is at play here.~~  
315 ~~One final possibility is that. Most likely, the electrical pulse to the hand is is responsible for a transient arousal~~  
316 ~~reaction, which could explain a generalized (spatially-unspecific) boost in performance.~~

317 Interestingly, the oscillatory component is also modulated over time, but in the opposite  
318 direction. The drop in performance – visible around 0.6 s after the nerve stimulation – is, in  
319 fact, paralleled by an increase in strength of the oscillatory modulation. At a first sight, this  
320 pattern of results appears surprising. Periodicity in behavior is typically interpreted as the  
321 consequence of two combined factors: 1. the influence of the peri-stimulus oscillatory phase –  
322 an index of neuronal excitability – on behavioral performance, and 2. the systematic phase-

323 alignment ~~of the ongoing oscillations~~ ~~to~~ ~~by~~ a reference event (here, the nerve stimulation) [see  
324 (VanRullen, 2016)]. Due to the intrinsic non-stationarities and dynamical properties of  
325 neuronal oscillations, the phase cannot, however, be preserved indefinitely (Kaplan et al.,  
326 2005); on the contrary, phase-locking to the nerve stimulation is conceivably disrupted over  
327 time, which in turn would cause the phasic modulations to become undetectable at the  
328 behavioral level. In brief, the oscillations in visual performance are expected to decrease rather  
329 than increase as a function of time from the peripheral stimulation. An intriguing possibility is  
330 that the ~~change in~~ ~~strengthening~~ of the behavioral oscillations ~~is~~ actually linked to the  
331 accompanying ~~slow trend~~ ~~worsening~~ in performance level, or, more precisely, to the putative  
332 ~~arousal~~ modulations ~~of arousal/attention~~ ~~it~~ ~~it~~ may reflect. Alpha-band activity is a well-known  
333 proxy of cortical excitability and task-related engagement (Jensen and Mazaheri, 2010;  
334 Klimesch, 2012). Increased alertness and attentional focus are generally associated with a  
335 reduction in power (desynchronization) of alpha-band oscillations (Sauseng et al., 2005), which  
336 is also predictive of subsequent performance (Haegens et al., 2011; Thut et al., 2006; van Ede  
337 et al., 2011). Moreover, several studies have shown that (nonvisual) task-irrelevant  
338 stimulations can induce transient enhancement of visual performance and cortical excitability  
339 (as measured by TMS-evoked phosphenes) (Feng et al., 2014; Ramos-Estebanez et al., 2007;  
340 Romei et al., 2009; Romei et al., 2013) and, most recently, desynchronization of the occipital  
341 alpha rhythm (Gleiss and Kayser, 2014; Hillyard et al., 2016; Stormer et al., 2016). In  
342 particular, suppression of alpha/mu and beta activity between ~0.15 s and 0.4/0.6 s after  
343 sensorimotor stimulation, and its subsequent rebound, have been reported not only in  
344 sensorimotor (Della Penna et al., 2004; Nikouline et al., 2000), but also in occipito-parietal  
345 areas (Bauer et al., 2006). Remarkably, these power modulations display a very similar  
346 temporal profile as that of the behavioral oscillations reported in the present study. We could  
347 thus speculate that the behavioral influence of the alpha phase is weakened shortly after the

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348 stimulation of the median nerve (between ~0.25 s and 0.6 s) due to the concomitant dampening  
349 of alpha power (possibly associated with a general improvement in performance), and boosted  
350 at later times (at ~0.6 s) as a consequence of the alpha rebound. The spectrotemporal dynamics  
351 that characterizes visual performance might thus be the result of a complex interaction between  
352 phase-reset and power modulations, both ~~triggered-accompanying~~ by the activation of the  
353 sensorimotor system. This would also support the general assumption that the functional  
354 impact of neuronal oscillations positively scales with their amplitude. It has to be noted that  
355 we cannot discard the possibility that the behavioral periodicity and the putative underlying  
356 phase-resetting of neuronal oscillations does not actually reflect a specific (sensorimotor-  
357 visual) interaction but rather an unspecific effect which also might be mediated by an arousal  
358 reaction. This consideration potentially affects many other studies showing that salient, supra-  
359 threshold stimuli can reset the rhythmic sampling of sensory information, as revealed by the  
360 ensuing periodicity in performance [see for example (Fiebelkorn et al., 2011; Romei et al.,  
361 2012)]. Nevertheless, in contrast with this account, some studies in the visual domain have  
362 reported spatially-selective effects (Fiebelkorn et al., 2013; Landau and Fries, 2012) and, more  
363 importantly, one study has shown in the somatosensory domain that subliminal (not  
364 consciously perceived) stimuli are equally effective (Baumgarten et al., 2017).

365 ~~Previous studies have shown that salient visual and auditory events can ‘reset’ the~~  
366 ~~rhythmic sampling of visual information, as revealed by the ensuing periodicity in visual~~  
367 ~~performance (Fiebelkorn et al., 2011; Fiebelkorn et al., 2013; Landau and Fries, 2012; Romei~~  
368 ~~et al., 2012; Song et al., 2014). Intriguingly, a recent study reveals that an analogous~~  
369 ~~phenomenon may take place also at the level of the (peripheral) motor system~~ (Wood et al.,  
370 2015). Alpha-band oscillations recorded in the muscle activity of the arm during preparation  
371 for a reaching movement are phase-reset by the presentation of a task-relevant visual stimulus.

372 suggesting that oscillation-based mechanisms might also be involved in fast sensorimotor  
373 transformations.

374 Recently, behavioral (Benedetto et al., 2016; Tomassini et al., 2015) and  
375 neurophysiological (Tomassini et al., 2017) evidence has ~~also~~ further suggested that  
376 endogenous sensorimotor processes might be capable of synchronizing ongoing visual  
377 rhythmicity ~~might be synchronized with sensorimotor processes~~ (Benedetto et al., 2016;

378 Tomassini et al., 2015). In these studies, motor activity was spontaneously initiated and the  
379 oscillations in visual perception, though being time-locked to the movement, emerged already  
380 before its onset (Tomassini et al., 2015; Tomassini et al., 2017). This is an interesting fact in  
381 itself, as it reveals the anticipatory and endogenous nature of the reported visual oscillations,  
382 but conceals their exact origin [i.e., whether they are driven by the sensorimotor system; see  
383 discussion in (Tomassini et al., 2015; Tomassini et al., 2017)]. Here, we show that stimulation  
384 of the median nerve induces long-lasting, alpha-band oscillations of low-level visual  
385 perception, in the absence of any endogenous movement-related process. The current data do  
386 not allow us to infer the exact nature of the neurophysiological mechanisms underlying the  
387 behavioral modulations, such as whether they are the result of phase alignment of ongoing  
388 visual activity, or alternatively, they reflect visual activity which is evoked by the nerve  
389 stimulation. Indeed, these two possible physiological accounts can be hardly dissociated [for a  
390 relevant discussion see, for example, (Makeig et al., 2002; Sauseng et al., 2007)]. Future studies  
391 combining behavioral and neurophysiological measures as well as sensitive analyses will be  
392 necessary to advance our understanding with respect to this issue. However, irrespective of the  
393 specific neuronal mechanism, ~~t~~his result does ~~suggests~~ that the sensorimotor system ~~may~~  
394 actually exerts a modulatory influence on visual oscillatory activity. In fact, the somatosensory  
395 and motor subdivisions of the nervous system associated with the hand are functionally and  
396 anatomically interconnected and both are activated by the median nerve stimulation with

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397 almost the same latency (Balzamo et al., 2004; Huang et al., 2000; Lemon and van der Burg,  
398 1979). On the one hand, the ascending somatic afferences reach precentral motor neurons both  
399 indirectly and directly (Krubitzer and Kaas, 1990; Lemon and van der Burg, 1979). This pattern  
400 of connections explains why neurons in the motor cortex show somatosensory receptive fields  
401 that are similar to those recorded in S1 (Fetz et al., 1980; Lemon and Porter, 1976). On the  
402 other hand, a significant part of the descending corticospinal projections originate from  
403 somatosensory and parietal regions suggesting a non-exclusive motor control role (Lemon,  
404 2008). This idea is supported by the observation that the large majority of corticospinal  
405 projections target intermediate spinal zones while only a small portion directly reach alpha  
406 motoneurons in the ventral horns (Morecraft et al., 2013). This suggests that the descending  
407 motor volley is presumably involved in the control of nociceptive, somatosensory, reflex,  
408 autonomic, and somatic motor functions (Lemon, 2008). All in all, anatomical data and  
409 neurophysiological characterizations of single unit responses support the idea that the  
410 somatosensory and motor neural circuitry form a single functional sensorimotor system, that  
411 can be accessed through the peripheral nerve stimulation.

412         However, the current alpha-band modulations contrast with the existing evidence from  
413 studies involving spontaneous movement initiation which consistently reported effects  
414 confined to lower (delta-theta) frequencies (Benedetto et al., 2016; Benedetto and Morrone,  
415 2017; Hogendoorn, 2016; Tomassini et al., 2015; Tomassini et al., 2017; Wutz et al., 2016).  
416 An interesting possibility is that the spectral diversity of the visual effects associated with the  
417 endogenous and exogenous activation of the sensorimotor system may index their functional  
418 differentiation.

419         Furthermore, phase-reset of ongoing oscillations by the median nerve stimulation has  
420 been reported in the monkey primary auditory cortex (A1; (Lakatos et al., 2007). Also in this  
421 case, the modulations showed a different spectral signature as compared to those observed here,

422 being concentrated within the delta, theta and gamma bands. Overall, these findings suggest  
423 that the spectral specificity of the inter-areal phase modulations might be conditional upon  
424 several factors, such as their functional significance (e.g., exogenous/endogenous) as well as  
425 the intrinsic resonant properties of the targeted cortex (e.g., visual/auditory).

426         We show that, not only the endogenous – as reported by previous studies – but also the  
427 exogenous activation of the somatomotor hand system is capable of aligning the phase of alpha  
428 oscillations in visual areas, inducing oscillations in visual perception whose temporal evolution  
429 resembles that of well-described power modulations of their neuronal counterparts. This  
430 demonstrates a causal role of the sensorimotor system in synchronizing visual oscillatory  
431 activity with consequences for perception. The present work suggests that oscillation-based  
432 mechanisms may sub-serve core (task-independent) sensorimotor integration functions.

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449 **Figure legends**

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451 **Figure 1.**

452 Schematic of the timeline of the trial. At variable delays between 0.5 and 1.5 s from the start  
453 of the trial (i.e., display of dynamic visual noise and fixation point on screen), bipolar electrical  
454 stimulation with monophasic square wave of 100  $\mu$ s is delivered on the volar aspect of the right  
455 wrist to stimulate the median nerve. A near-threshold Gabor (1 c/deg), tilted by  $\pm 45$  deg, is  
456 briefly presented for 0.033 s (two frames) below fixation at random times (in steps of 0.033 s)  
457 in the range from 0.05 to 1.15 s after the median nerve stimulation. Visual performance is  
458 therefore sampled at  $\sim 30$  Hz within 1.1 s. In addition, the Gabor could also appear at one of  
459 three randomly chosen time points before the electrical pulse (-0.25, -0.15 and -0.05 s) with an  
460 overall probability of 15%. The snapshot shows a right-tilted Gabor as an example (for  
461 illustrative purposes visual contrast is higher than what used in the experiment) and the white  
462 square drawn in the top left corner where the photodiode was positioned.

463

464 **Figure 2.**

465 **a. Group-level** Average performance (% of correct responses) in the visual orientation  
466 discrimination task as a function of time from the median nerve stimulation (zero time by  
467 definition). The gray shaded area represents the standard error of the mean. The dashed  
468 horizontal line indicates threshold level (75% correct). **b.** top. Colored lines show the best-  
469 fitting linear functions for the individual time courses of visual performance. The black line  
470 represents the linear function which best fitted the average time course (displayed in a). bottom.  
471 Bars show average visual performance within the first (0.05-0.6 s; dark gray) and the second

472 (0.6-1.15 s; light gray) part of the tested time window after the nerve stimulation (\*\*\*)  
473  $p < 0.0001$ , paired sample two-tailed t-test). Error bars show standard errors of the mean.

474 **Figure 3.**

475 Detrended time course of visual performance following the median nerve stimulation,  
476 calculated on the data pooled across subjects (left panel). Power spectrum ~~of~~ the detrended  
477 visual performance pooled across subjects (time series shown in the left panel) calculated by  
478 means of the fast Fourier transform (FFT; right panel, black line). The solid gray line indicates  
479 the mean of the surrogate spectral distribution and the dashed gray line the upper limit of the  
480 95% confidence interval (\*  $p < 0.05$ , FDR-corrected for multiple comparisons across  
481 frequencies).

482

483 **Figure 4.**

484 Time-frequency power plot of the visual performance (~~calculated by pooling the data~~ across  
485 subjects; same time series shown in Figure 3, left panel) after the median nerve stimulation  
486 (left panel). The black lines in the small insets show the power as a function of frequency  
487 (averaged across time points in the range 0.05-1.15 s; left inset) and as a function of time  
488 (averaged across frequencies in the range 4-14.5 Hz; top inset). The large inset illustrates the  
489 time course of the power at 9.5 Hz (significant time points – after FDR correction – are marked  
490 by black dots).

491

492 **Figure 5.**

493 Predictive value for the visual performance (estimated with Jackknife) of sinusoidal functions  
494 with frequencies between 1.5 and 14.5 Hz (left panel; see random-effect analysis described in  
495 the Methods). The gray shaded area represents the jackknife standard error (\*  $p < 0.05$ , FDR-  
496 corrected for multiple comparisons across frequencies). Across-subject distribution of the

497 optimal phase angles (the phases associated with the highest performance) for the alpha  
498 frequency reported as statistically significant in the group-level analysis (i.e., 10.5 Hz). The  
499 black line represents the mean resultant vector.

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