Inhibitory interactions between the visual and motor systems during optokinetic stimulation and simultaneous dynamic handgrip exercise

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Highlights

- Motor activation can inhibit the visual system even during continuous visual stimulation.
- Continual visual input produces sustained inhibitory influence on the motor system.
- EEG can be reliably assessed during nystagmus.

Abstract

Objectives: Inhibitory interactions between the visual and motor systems have been observed during transient stimulation of either system. However, it is unknown how inhibition operates during simultaneous and continuous engagement of both systems.
Methods: We presented right-handed participants (n = 14) with optokinetic stimulation (OKS), with and without a simultaneous dynamic handgrip exercise. We assessed the EEG upper-alpha band (10-12 Hz) to investigate inhibitory interactions, and explored their effect on optokinetic nystagmus (OKN).
Results: OKS + handgrip simultaneously produced motor activation and visual inhibition, compared to OKS alone. Meanwhile, the velocity of OKN increased, selectively during left handgrips. OKS without handgrip produced simultaneous visual activation and motor inhibition compared to an open-eyes baseline. The open-eyes baseline itself increased motor peak-frequency towards the inhibitory upper-alpha range compared to closed eyes.
Conclusions: Motor activation inhibited the visual system even during visual stimulation. This inhibition likely disrupted visual processing, triggering an OKN speed-up to relocate the OKS. Increasing visual input produces increasing motor inhibition.
Significance: These observations extend previous results in standard settings and confirm the reliability of EEG in conditions involving nystagmus, important in clinical vestibular research. Visual inhibition through handgrip could be a candidate for developing rehabilitation from visually induced dizziness.

Keywords: Optokinetic stimulation, EEG, peak frequency, alpha, handgrip, sensorimotor interaction

Abbreviations. OKS: Optokinetic stimulation; OKN: Optokinetic nystagmus

1. Introduction

Mutually inhibitory interactions between the visual and the motor systems have been classically shown when either one of them is engaged transiently and /or in isolation (e.g. Becker-Bense et al., 2006, Cross-Villasana et al., 2016, Delorme et al., 2007, Koshino and Niedermeyer, 1975, Pfurtscheller and Lopes da Silva, 1999). The function of this mutual inhibition is presumed to facilitate attention to the stimulated sensory modality by down-regulating the other modality (Crabtree and Isaac, 2002, Kober et al., 2015, Sterman, 1996). This leaves the open question as to how such mutual inhibition plays out when both the visual and motor systems are engaged simultaneously.

As seen in classic EEG studies, the execution of isolated hand movements leads not only to activation of the motor cortex but also simultaneous down-regulation of the visual cortex (e.g. Gerloff et al., 1998, Pfurtscheller and Lopes da Silva, 1999). This phenomenon can also be observed over longer time periods during the execution of dynamic handgrip exercise (Cross-Villasana et al., 2016) or during a button-pressing sequence (Deiber et al., 2001). The opposite phenomenon, down-regulation of the motor cortex by the visual cortex, has been observed in the EEG when a word to read is presented on screen (Pfurtscheller and Lopes da Silva, 1999), during visual pattern exploration (Koshino and Niedermeyer, 1975) or through the presentation of flickering lights (Brechet and Lecasble, 1965). Brain stimulation studies have suggested that increasing visual activation even just by opening the eyes reduces motor excitability (Leon-Sarmiento et al., 2005, Strigaro et al., 2015).

Electrophysiological evidence suggests that such mutual sensory inhibitory interactions arise at the thalamic level, where different sensory pathways can exert inhibitory modulation on each other via the thalamic reticular nucleus (TRN; Crabtree and Isaac, 2002, Edlow et al., 2012, Guillery and Harting, 2003, Zikopoulos and Barbas, 2007). In this account, when a thalamic nucleus relays a signal from a particular sensory stream towards the cortex, its axon collaterals simultaneously stimulate sections of the TRN that in turn down-regulate relay nuclei of other sensory modalities (Crabtree and Isaac, 2002, Guillery and Harting, 2003, Zikopoulos and Barbas, 2007). As the TRN also mediates the generation of the cortical alpha rhythm (Hughes and Crunelli, 2005, Larson et al., 1998, Vijayan and Kopell, 2012), the result of inter-sensory inhibitory influence may be reflected on surface EEG as an alpha power enhancement over the inhibited system (Pfurtscheller and Lopes da Silva, 1999, Steriade, 2000, Sterman, 1996). Furthermore, it has been observed that stimulation of one thalamocortical pathway can interrupt ongoing activity in another pathway through TRN-mediated inhibition in the thalamus (Crabtree and Isaac, 2002, Zikopoulos and Barbas, 2007). Therefore, such interference between already active thalamocortical streams should also be observable over scalp EEG alpha measurements. This proposal could be examined by testing for the classic visual down-regulation produced by hand-movements, but during active visual stimulation. Modulation of the visual and motor systems throughout can then be tracked by time-frequency analysis of the EEG alpha band. In particular, in the upper-alpha band, amplitude enhancements are indicative of cortical inhibition and amplitude decrements reflect activation (Hummel et al., 2002, Klimesch et al., 2007, Pfurtscheller and Lopes da Silva, 1999, Zarkowski et al., 2006).

Here we implement steady activation of the visual system through OKS, which is then paired with simultaneous motor activation through dynamic-handgrip exercise (Kluess et al., 2000) as used in a previous experiment (Cross-Villasana et al., 2016). OKS in the current study consists of a series of moving stripes presented on a screen, which induce a reflexive eye movement that repetitively tracks their motion (Ventre-Dominey and Luyat, 2008), called optokinetic nystagmus (OKN; Ilg, 1997). During OKN, the eyes follow the direction of OKS through a slow-phase movement, which is followed by a quick reset in the opposite direction, called the quick-phase, followed again by a slow phase, and so on (Ilg, 1997, Ventre-Dominey and Luyat, 2008). Like other visual stimuli, OKS has reliably been shown to induce visual-cortical activation in EEG (Gulyas et al., 2007, Magnusson et al., 1985) and fMRI (Becker-Bense et al., 2006, Bense et al., 2001, Dieterich et al., 2003, Kikuchi et al., 2009). Considering the visual downregulation that dynamic handgrip may produce, opposing OKS activation, we expected this may lead to a reduction of the OKN slow-phase velocity (Magnusson et al., 1985).

From the OKS-fMRI studies, Becker-Bense et al. (2006) incidentally observed that apart from visual activation, OKS also down-regulated motor areas, similar to the effects seen in EEG studies with different visual stimuli (Brechet and Lecasble, 1965, Koshino and Niedermeyer, 1975, Pfurtscheller and Lopes da Silva, 1999). However, previous OKS-EEG studies did not assess anterior regions (Gulyas et al., 2007, Magnusson et al., 1985), hence it is unclear whether any inhibitory processes (alpha power increases) are observable at central and anterior locations during OKS. This absence of evidence may be due to the problem of the unavoidable eye-movement artefacts in the EEG induced by OKN (Gulyás et al., 2007), which are stronger at anterior regions. However, recent advances allow to circumvent this problem through techniques such as independent component analysis (ICA), used to separate out eye-movement components (Bell and Sejnowski, 1995, Makeig et al., 1995). Spatial filters like the surface Laplacian further reduce volume conduction and help to specify the location of experimental effects (Kayser and Tenke, 2015, Tenke and Kayser, 2005). Therefore, to deal with eye movements, those same techniques are extended in the current design, as has been done in a previous study (Cross-Villasana et al., 2018).

Within the current design, detecting the classic bilateral motor activation (alpha reduction) produced by hand movements (e.g. Cross-Villasana et al., 2016, Pfurtscheller and Lopes da Silva, 1999) but during simultaneous OKN, would support the reliability of EEG measurement. Once EEG reliability is demonstrated, we proceed to investigate our main experimental aims: the inhibitory interference of motor activity with visual processing during OKS, its effects on OKN, and the inhibitory influence of isolated OKS over motor regions.

2. Materials and methods

2.1 Study design

We compared the effects of simple OKS exposure with the effects of simultaneous OKS/dynamic handgrip, on the EEG upper-alpha band (10-12 Hz), and on the slow-phase velocity of OKN. Oscillations were tracked throughout OKS using time-frequency analysis. OKN was assessed via eye-tracking. Electro-oculography (EOG), electromyography (EMG) and grip-force measurements were used as control variables. Our main experimental hypotheses are summarized in Table 1.

During simultaneous OKS-Dynamic Handgrip
1. The motor system shows reduced upper-alpha amplitude (activates) during OKS + left or right Handgrip compared to OKS alone (supporting reliable EEG measurement during OKN).
2. The visual system shows increased upper-alpha amplitude (deactivates) during OKS + left or right Handgrip compared to OKS alone.
3. OKN slow-phase velocity is reduced during OKS + left or right handgrip compared to OKS alone.
During increasing visual input towards OKS alone
4. The visual system shows reduced upper-alpha amplitude (activates) with increasing visual input, from eyes closed baseline, to eyes open baseline, to OKS.
5. The motor system shows increased upper-alpha amplitude (deactivates) with increasing visual input, from eyes closed baseline to eyes open baseline, to OKS.

Table 1. Summary of the experimental hypotheses.

The experiment was designed to be short-lasting to prevent effects of tiredness or boredom on the measurements, especially on the EEG. It consisted of six blocks and two baselines with small breaks in between, lasting around 15 min altogether. Only right-handed participants were included in

the study. Laterality was assessed with the Flinders Handedness Survey (Nicholls et al., 2013), where scores between 5 and 10 reflect right-handedness.

2.2 Participants

From nineteen recruited participants, five were excluded: one participant could not perform dynamic handgrip, one showed no clear nystagmus, one had an incomplete eye-tracking recording, and two had incomplete EMG recordings. The final sample consisted of 14 participants (7 female) with a mean age of 26 years (range: 23–30 years). Their mean laterality quotient was 9.5 (range: 5–10) in the Flinders Laterality Inventory. The study was approved by the ethics committee at the medical faculty of LMU Munich.

2.3 Procedure

Before the experiment, two EEG resting baselines were measured: an eyes-closed baseline (BLC) and then an eyes-open baseline (BLO), each 60 secs long and performed while fixating a white cross. Afterwards, EMG and grip-force baselines were assessed, where participants performed a single grip of maximum voluntary contraction (MVC) with either hand on the digital dynamometer (Kluess, Wood, and Welsch 2000; Liu et al. 2003). The main experiment consisted of six blocks. In each block, first a white fixation cross appeared for 5 seconds at the center of the screen, followed by 45 seconds of OKS, followed again by 60 seconds of fixation cross presentation to dissipate possible task-aftereffects before the next block. A chin-rest was used to stabilize the participants' head with their eyes at the center-level of the screen. Screen edges were covered with a black rectangular cardboard frame, leaving a 28° x 13° (visual angle) visible screen background. OKS was presented on an LCD monitor (1680 x 1050 pixel resolution) with a refresh rate of 60 Hz, placed at 40 cm from the participant. OKS stimuli consisted of 19 black (RGB: 0, 0, 0) and 19 white (RGB: 255, 255, 255) bars (bar width 2.3 cm/3.3°) which travelled rightwards at 33°/s. After each block, participants took a brief break until they felt ready for the next block. The first experimental block always consisted of OKS without handgrip. This was done to assure proper EEG characterization of modulations induced by OKS, without possible effects of tiredness, boredom, or aftereffects from previous blocks. The second and third blocks consisted of combined OKS with Left handgrip (OKS+L) and OKS with Right hand grip (OKS+R), order counterbalanced. After the third block, the process was repeated, with the fourth block always being OKS alone, and the fifth and sixth blocks of counterbalanced OKS+L and OKS+R. In the handgrip blocks, during the initial 5 seconds fixation cross, participants held the dynamometer passively with one hand, the other resting on their lap, palm facing down. Participants were then instructed to repeatedly squeeze the hand-dynamometer at OKS onset, firmly as if "trying to make a fist", at approximately 2 Hz, with a force that they could sustain for 45 s. No displays of force and frequency of the handgrip were presented to the participant, since these might distract attention from the OKS and interrupt the ongoing OKN. The assessed grip-force and EMG data were analysed to ensure compliance with the task and to verify comparable effort exertion with each hand. During the last 60 seconds of fixation cross, the dynamometer was removed by the experimenter and both hands rested on the lap. Once the data was processed, the two blocks of each condition (OKS, OKS+L, OKS+R) were compared to each other. Since no significant differences were found between the two sets of blocks, each set was averaged together for final analysis.

2.4 Physiological measurements

2.4.1 EEG and EOG

EEG was amplified using a BrainAmp DC amplifier (Brain Products, Munich, Germany) with a sampling rate of 1000 Hz, a band pass filter from 0.1 to 250 Hz and a notch filter at 50 Hz. The data

was collected with 64 sintered Ag/AgCl ring electrodes mounted on an elastic cap (EASYCAP GmbH, Germany). 61 electrodes of the international 10/10 system were used for EEG recording (FP1, FPz, FP2, AF7, AF3, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, TP10, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, POz, PO4, PO8, O1, Oz and O2). Two electrodes were used to record horizontal EOG, placed on the outer canthi of the left and right eyes. Vertical EOG was recorded from one electrode below the observer's left eye and from FP1. All electrode impedances were kept below 5 kΩ, referenced online to the left mastoid (TP9), with the ground electrode on position AFz.

Subsequent EEG and EOG processing was carried out with Brain Vision Analyzer 2.1 (Brainproducts, Germany). Data was digitally filtered between 0.1 and 40 Hz with a notch filter enabled at 50 Hz using an infinite-impulse-response filter (Widmann et al., 2015). Visual inspection of the data allowed rejecting segments with large mechanical artefacts. Nystagmus and other eye movements' artefacts in the EEG were corrected using an infomax ICA as implemented in Brain Vision Analyzer 2.1 (Bell and Sejnowski, 1995, Makeig et al., 1995), which ran on the entire dataset. High-energy components reflecting nystagmus, blinks or other eye movements were manually removed. Afterwards, data was re-sampled to a power of 2 (1024 Hz). Before segmentation, EEG data was converted to a reference-free scheme through a Surface Laplacian estimation, using a spline order $m = 4$ and smoothing constant $\lambda = 0.00001$. Such parameters serve to reduce volume conduction, attenuating the effect of any remaining nystagmus artefact on the EEG and enhancing the location precision of experimental alpha modulations.

The data was segmented into each condition: BLC, BLO, OKN, OKN+L and OKN+R, each segment lasting 45 sec. Time-frequency analysis was implemented on pre-selected electrodes C3-C4 for the motor system, and O1-O2 for the visual system. The segmented blocks were convolved with 10-cycle complex Morlet wavelets, scaled logarithmically in 30 steps between 5 and 15 Hz. These parameters were set to maximize frequency precision over time precision. For statistical analysis, the spectral amplitude of 6 wavelet layers corresponding to the upper-alpha band were extracted, with central frequencies of 10.27, 10.67, 11.08, 11.51, 11.95 and 12.41 Hz, across the whole 45 seconds of the corresponding block. The 6 layers were then averaged together for each subject. The resulting average at each electrode was then pooled together for the motor region (C3-C4) and visual region (O1-O2).

To achieve a topographic representation of our results, scalp-maps were derived from fast-fourier transformations (FFT) over the entire 45 second segments, and contrasted between experimental conditions. To compute FFT, each 45 sec segment was segregated into 2 sec contiguous epochs, spectral amplitudes were extracted using a Hamming window with 50% overlap between contiguous epochs, allowing a spectral resolution of 0.5 Hz. All epochs within each of the 45 segments were averaged together at each electrode to create the final spectral distribution. Since FFT misses the temporal dynamics of cortical modulations along 45 seconds, no statistical analyses were performed on FFT data, only on the wavelet transformed data.

2.4.2 EMG and Grip Force

Surface EMG was recorded using an ExG bipolar amplifier (Brain Products, Germany) connected to the EEG amplifier, sharing recording settings. Ag/AgCl electrodes were placed in bipolar montage on the skin over the flexor digitorum superficialis (FDS) of the left and right arm, with the ground placed near the lateral epicondyle of the elbow of the corresponding arm. Handgrip force was assessed with a digital hand dynamometer (Vernier, Beaverton, USA) connected to an independent computer running the Vernier Graphical Analysis software. The sampling rate was 10 Hz. One participant's grip force data and another participant's EMG data were lost through technical error. For analysis the EMG data of the maximum voluntary motor contractions (MVC) and the 45 sec periods of OKS-dynamic-handgrip of each hand were rectified and exported. MVC for both EMG and dynamometer grip force recordings was defined as the maximum peak achieved during the maximal contraction period of the respective hand. For dynamic handgrip, all data points of the 45 sec block were averaged together and normalized to the corresponding left or right MVC.

2.4.3 Eye tracking

Eye movements were recorded by head-mounted video-oculography of the left eye with a sampling rate of 220 Hz (EyeSeeCam system, EyeSeeTec, Germany). The data was analysed offline through a custom MATLAB script, where blinks were first removed before detection of nystagmus quick phases, defined as eye velocity greater than 10 °/s and absolute acceleration greater than 300°/s². The start point was determined at the time of peak velocity. The end point was considered when the eye velocity values reached 0°/s, indicating a change in the eye direction and the beginning of the slow phase (SP) of nystagmus used for analysis.

2.5 Data analyses

We first analysed the effects of simultaneous OKS-dynamic handgrip, where upper-alpha amplitudes were submitted to a 2x3 repeated measures ANOVA with factors "region" (motor, visual) and "condition" (OKS,OKS+L,OKS+R). The Greenhouse-Geisser correction was used when necessary to adjust for violations of sphericity. Afterwards, the relevant hypotheses stated in Table 1 were tested through directed post-hoc *t*-tests, with effect-sizes assessed through Cohen's d_z (Lakens, 2013). For the slow-phase velocity of OKN, a repeated measures ANOVA with the factor "condition" (OKS, OKS+L, OKS+R) was implemented with subsequent post-hoc *t*-test comparisons pertinent to experimental hypotheses. To control for the amount of muscular activation, the normalized grip-force and EMG levels were compared during OKS+L and OKS+R, expecting no significant differences between them.

Secondly, we analysed the effects of increasing visual input and OKS alone by submitting the upper-alpha amplitudes to a 2x3 ANOVA with repeated measures on the factors "region" (motor,visual) and "condition" (BLC, BLO, OKS). Likewise, the stated hypotheses in Table 1 regarding increasing visual input and OKS alone were tested through directed pairwise *t*-tests.

3. Results

Fig. 1 displays the wavelet-derived upper-alpha amplitudes at each analysed electrode grouped for motor and visual regions, along all experimental conditions. Each condition adds incremental load on the participant from resting with eyes closed in BLC, opening the eyes in BLO, then perceiving OKS, and finally simultaneous OKS and dynamic handgrip with left in OKS+L or right in OKS+R. Fig. 2 presents the contrasts between these conditions accompanied by a topographic representation derived from FFT.

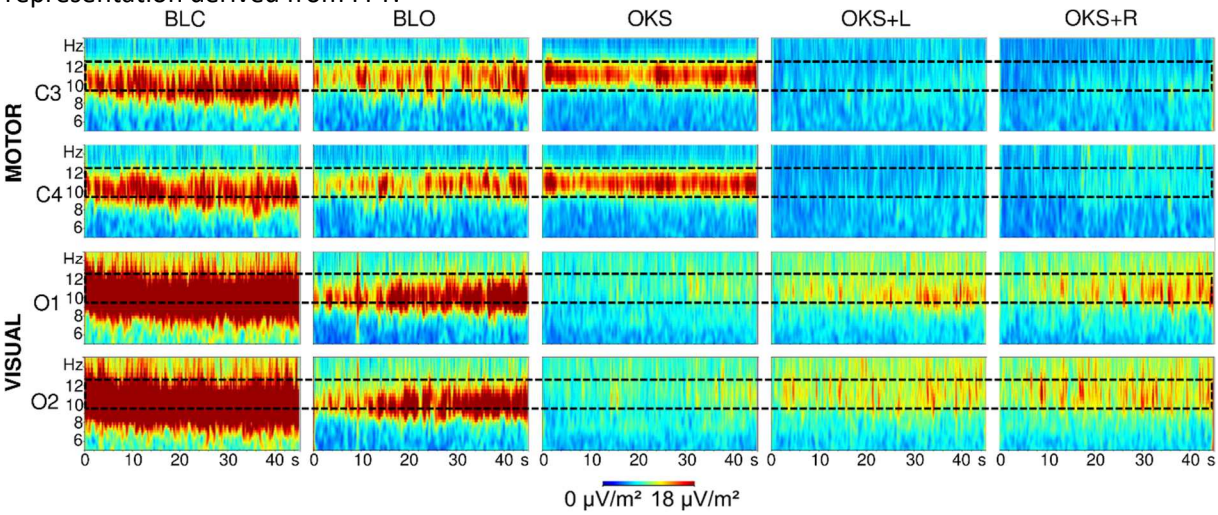

Fig. 1. Grand average alpha amplitudes at the motor electrodes C3-C4 (motor region) and visual electrodes O1-O2 (visual region) extracted through 45 sec wavelet analysis of the different experimental conditions. The dashed rectangle highlights the upper-alpha sub-region (10 -12 Hz) used for statistical analysis. The conditions are presented from less, to more load on the participant:

BLC = Baseline closed eyes; BLO = Baseline open eyes; OKS = Optokinetic stimulation; OKS+L = Optokinetic stimulation + Left handgrip; OKS+R = Optokinetic stimulation + Right handgrip.

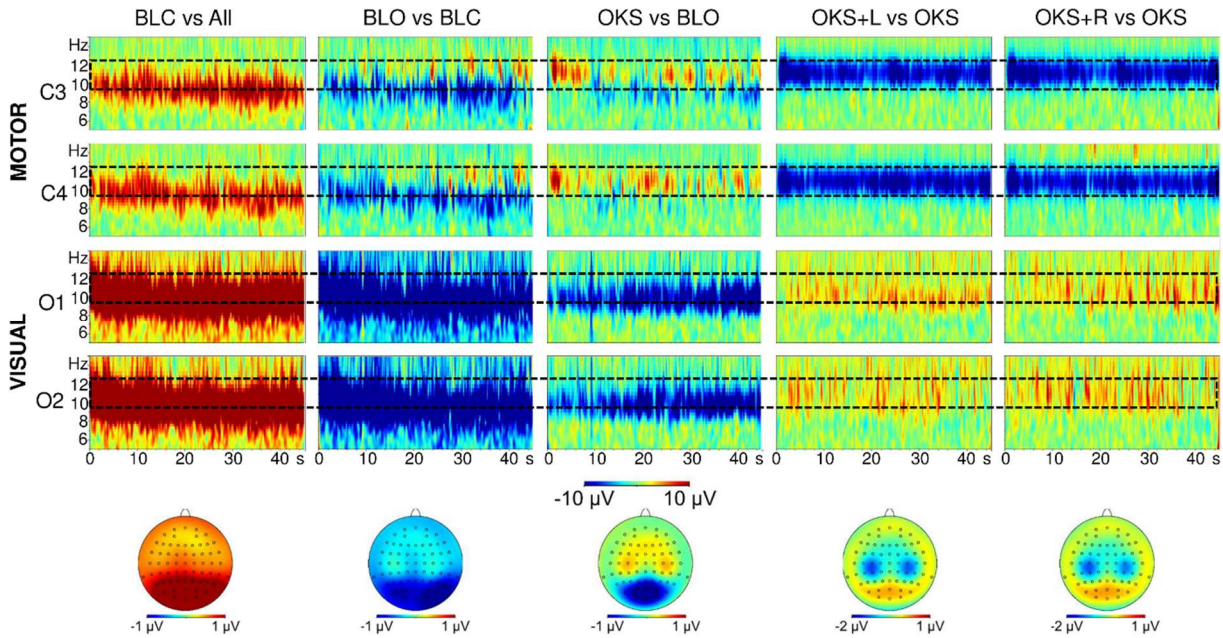

Fig. 2. Contrasts of grand average alpha amplitude levels between consecutive experimental conditions. The conditions are presented from less, to more load on the participant: BLC vs all = Baseline closed eyes minus the average of all other conditions. BLO vs BLC = Baseline eyes open minus baseline eyes closed; OKS vs BLO = optokinetic stimulation minus baseline eyes open. OKS+L vs OKS = Optokinetic stimulation with left dynamic handgrip minus optokinetic stimulation. OKS+R vs OKS = Optokinetic stimulation with right dynamic handgrip minus optokinetic stimulation. Time-frequency representations are derived from wavelet analysis, grouped as in Fig. 1. The topographic representations below are derived from FFT over the entire blocks.

3.1 Effects during simultaneous OKS-Dynamic Handgrip

First the effects of handgrip were analysed to assess reliable EEG measurement. A significant effect of "condition" was observed [$F(1.041, 13.53) = 5.92$, $p < .05$, $\eta^2 = .313$] , showing that OKS, OKS+L and OKS+R produced differences in upper-alpha amplitude. Table 2 shows the means and standard deviations of upper-alpha amplitude. Directed post-hoc t-tests are summarized in Table 3. They show that OKS+L and OKS+R significantly reduced upper-alpha amplitude at motor regions compared to OKS. This implies that dynamic-handgrip with either hand produced a detectable activation of motor areas, confirming our first hypothesis that motor activation is detectable during nystagmus, and supporting the reliability of EEG assessment in this condition. This amplitude reduction can be clearly appreciated in Fig. 1, where the motor alpha oscillations in OKS disappear during OKS+L and OKS+R. The contrast in Fig. 2 further reflects this dramatic reduction in OKS+L vs OKS and OKS+R vs OKS. As seen on Table 3, *t*-test comparisons for the visual region showed significantly greater alpha amplitudes during OKS+L and OKS+R than during the OKS condition. This confirms our second hypothesis, where handgrip execution had an inhibitory influence over the visual cortex even during visual stimulation. In Fig. 1, it can be appreciated how the introduction of OKS makes alpha disappear at the occipital locations O1 and O2, but return during OKS+L and OKS+R. The contrast in Fig. 2 further emphasizes greater alpha amplitudes at O1 and O2 in OKS+L vs OKS and OKS+R vs OKS.

An interaction between "condition" and "region" [$F(1.031, 13.41) = 14.60$, $p < .01$, $\eta^2 = .529$], indicates that the experimental conditions also induced amplitude differences between the regions. This was driven by the effects described above having opposite directions, where the motor electrodes C3-C4 decreased alpha amplitude during simultaneous OKS and handgrip, and visual

electrodes O1-O2 increased it. No main effect was observed for "region" [F(1, 13) = 1.74, p = .21, η^2 = .118] indicating no mean difference in amplitudes between regions across all experimental conditions.

	OKS	**OKS+L**	**OKS+R**
Motor region	14.00 (2.73)	5.74 (.67)	6.09 (.64)
Visual region	8.19 (1.09)	10.67 (1.44)	11.06 (1.59)

*Table 2.*Mean (SE) upper-alpha amplitudes for each electrode averaged for 45 seconds at each condition. OKS = Optokinetic stimulation; OKS+L = OKS + Left handgrip; OKS+R = OKS + Right handgrip.

	OKS vs OKS+Left		**OKS vs OKS+Right**	
	t(13)	d_z	*t*(13)	d_z
Motor region	3.37**	.90	3.29**	.88
Visual region	-3.70**	.99	-3.90**	1.04

Table 3. t -scores and effect sizes for differences in upper-alpha amplitude between the isolated OKS with each of the OKS+Left and OKS+Right handgrip.
* indicates significance p < .05
** indicates significance p < .01

Regarding OKN, a significant effect for "condition" was observed [F(1.40, 18.18) = 4.20, p < .05, η^2 = .244], indicating differences in the slow-phase velocity of OKN between the experimental conditions. Post-hoc *t*-tests indicated a significant increase during OKS+Left (M=15.44, SE=1.42) compared to OKS (M=13.40, SE=1.46), *t*(13)=−2.75, p=.017, d_z =−0.74. This is contrary to our third hypothesis, which predicted that the alpha enhancement produced by handgrip would be related to a *reduction* in slow-phase velocity. The effect was specific to left handgrips, as OKS+Right (M=14.64, SE=1.40) was not significantly faster than isolated OKS *t*(13)= −1.43, p=.18, d_z = −0.38. Meanwhile, the slow-phase velocity did not differ between OKS+Left and OKS + Right, *t*(13)= 1.78, p=.10, d_z = 0.48.

Regarding gripping force, there were no significant differences between %MVC for the left (M=27.95, SE=2.41) and for the right hand (M=24.87, SE=1.40), *t*(12)=1.51, p=.16, d_z = *0.4*. In EMG, there was also no significant difference %MVC for the left (M=17.31, SE=2.79) than for the right hand (M=21.29, SE=2.86), *t*(12)=-1.79, p=.10, d_z = -0.5. In this way, gripping force and EMG measures suggest that participants exerted comparable effort with each hand, ruling out any confounding difference in force.

3.2 Effects during increasing visual input and OKS alone

Having confirmed that the EEG assessment during OKN is reliable, we proceeded to analyse the effects of increasing visual input and OKS alone over visual and motor regions. Repeated measures ANOVA over upper-alpha amplitudes revealed a significant effect of "condition" [F(1.18, 15.37) = 41.01, p < .001, η^2 = .76]. As seen in Table 4 and Table 5, post-hoc *t*-tests revealed significantly lower amplitudes in the visual region on BLO than BLC, and OKS than BLO. This confirms the fourth hypothesis that, besides alpha reduction after eye opening, OKS would produce further alpha reduction, reflecting visual activation as in previous EEG and fMRI studies. Fig. 1 shows how elevated alpha levels at visual electrodes O1 and O2 during BLC are reduced during BLO and disappear during OKS. Fig. 2 contrasts confirm these observations.

	BLC	**BLO**	**OKS**
Motor region	13.38 (2.31)	12.32 (2.48)	13.99 (2.73)
Visual region	30.43 (4.34)	14.26 (2.01)	8.19 (1.09)

Table 4. Mean (SE) upper-alpha amplitudes for each electrode averaged for 45 seconds at the conditions: BLC= Baseline eyes closed BLO = Baseline open eyes; OKS = Optokinetic stimulation.

	BLC VS BLO		BLO VS OKS	
	$t(13)$	d_z	$t(13)$	d_z
Motor region	1.01	.27	-2.39*	.64
Visual region	6.16**	1.65	4.70**	1.26

Table 5. t -scores and effect sizes for differences in upper-alpha amplitude between the conditions with increasing visual input. BLC = Baseline closed eyes; BLO = Baseline open eyes; OKS = Optokinetic stimulation.
* indicates significance p < .05
** indicates significance p < .01

A comparison between the BLC and the BLO conditions at the motor region showed no significant amplitude enhancement (Table 5), so that inhibition over the motor area was not evident after eye opening. However, when comparing BLO to OKS, a significant enhancement did appear, so that visual stimulation enhanced motor upper-alpha amplitude. In this way, our fifth hypothesis, that increasing visual input would produce greater inhibition over motor areas was only partially confirmed. However, a close inspection of Fig. 1 suggests that increasing visual input by eye opening in BLO and further OKS lead alpha oscillations to concentrate specifically in the inhibitory upper-alpha range, although perhaps BLO amplitude did not always surpass the broad alpha levels during BLC. When averaging the amplitude of each frequency layer in Fig. 1 across the entire 45 sec of each experimental condition (Fig. 3), it can be confirmed that BLO and OKS peak at faster frequencies than BLC, despite BLO not surpassing BLC amplitude on average. Such peaks also lie within the inhibitory upper-alpha region. These observations prompted us to analyse changes in peak frequency (rather than amplitude) over motor electrodes with increasing visual input.

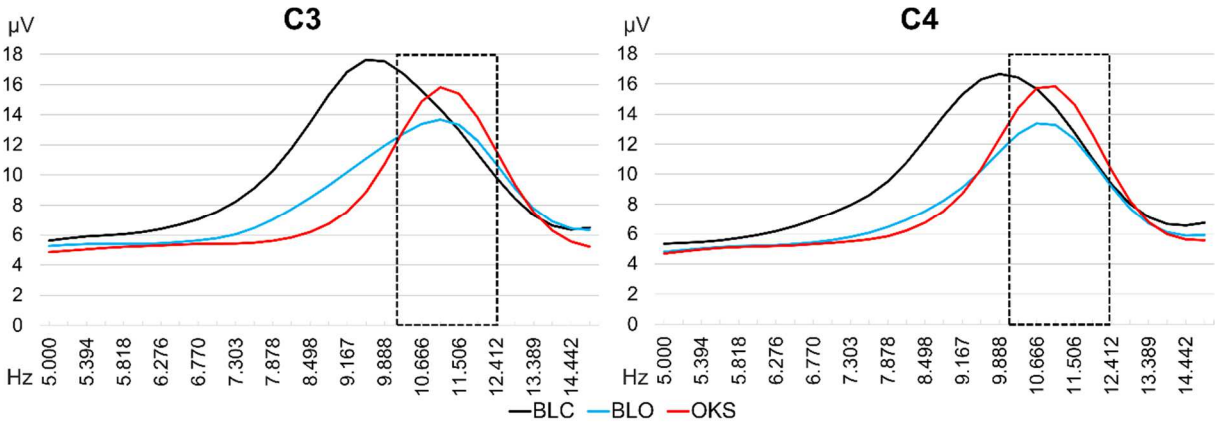

Fig. 3. Amplitude distribution extracted from wavelet analysis at motor electrodes C3 and C4, averaged for the 45 sec of each condition. The dashed rectangle highlights the upper-alpha regions used for analysis. BLC = Baseline closed eyes; BLO = Baseline open eyes; OKS = Optokinetic stimulation.

3.3 Peak frequency changes over motor regions with increasing visual input

Fig. 4 displays the peak frequency at every data point (Wei, 2007) from the grand averaged time-frequency analysis displayed in Fig. 1 for the BLC, BLO and OKS conditions over motor electrodes C3 and C4. It can be observed that slower peak frequencies of around 8 to 10 Hz during BLC, broaden their range to include faster frequencies during BLO and finally concentrate around 11 Hz during OKS. After extracting the individual peak frequencies from each participant's wavelet analysis at each condition, we implemented a 3x2 repeated measures ANOVA with the factors "condition" (BLC, BLO, OKS) and "electrode" (C3 and C4). Results showed a main effect of "condition" [$F(2, 26) = 12.47$, $p < .001$, $\eta^2 = .49$], implying that each of the experimental conditions produced a change in the peak frequencies at each electrode. Table 6 displays the mean peak frequencies at

each phase, while Table 7 shows the results of post-hoc *t*-tests. It can be observed that BLO and OKS showed significantly faster peak frequencies than BLC, within the upper alpha range. Meanwhile, peak frequencies did not differ between BLO and OKS. These observations support that increasing visual input biases oscillations towards the inhibitory upper-alpha range. As seen in the previous section, once in the upper-alpha range, greater visual input increases upper-alpha amplitude.

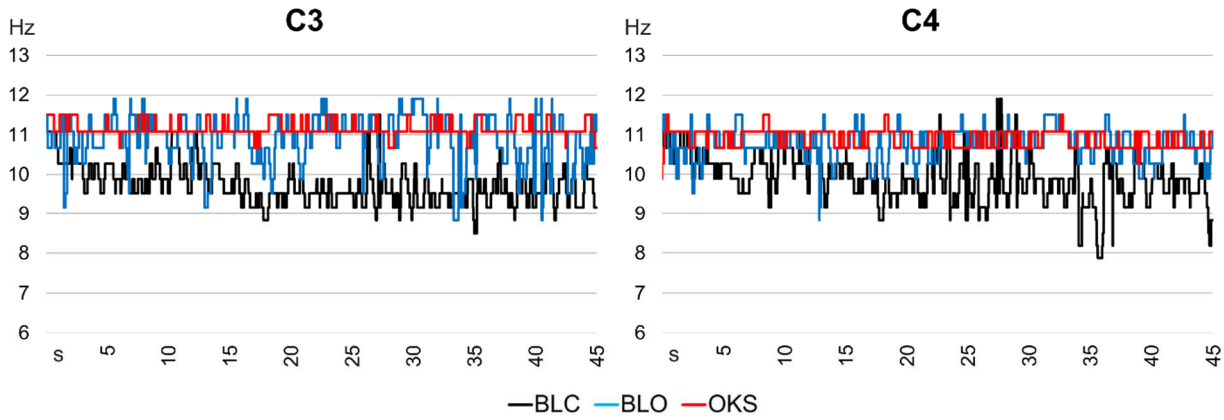

Fig. 4. Peak frequencies at the motor electrodes C3 and C4 in the motor region during experimental conditions with increasing visual input. The conditions are overlaid with each other. BLC = Baseline closed eyes; BLO = Baseline open eyes; OKS = Optokinetic stimulation.

	BLC	**BLO**	**OKS**
C3	10.55 (.26)	11.44 (.23)	11.38 (.16)
C4	10.62 (.22)	11.26 (.19)	11.20 (.18)

Table 6. Mean (SE) peak frequencies for each electrode averaged for 45 seconds at the conditions: BLC= Baseline eyes closed BLO = Baseline open eyes; OKS = Optokinetic stimulation.

	BLC VS BLO		**BLC VS OKS**		**BLO VS OKS**	
	t(13)	d_z	*t*(13)	d_z	*t*(13)	d_z
C3	-4.45**	1.19	-4.23**	1.13	0.36	0.10
C4	-3.31**	0.88	-2.92*	0.78	0.57	0.15

Table 7. t -scores and effect sizes for differences in peak frequency between the conditions with increasing visual input. BLC = Baseline closed eyes; BLO = Baseline open eyes; OKS = Optokinetic stimulation.
* indicates significance $p < .05$
** indicates significance $p < .01$

An interaction between "electrode" and "condition" [$F(2, 26) = 3.44$, $p < .05$, $\eta^2 = .21$] indicates that the experimental conditions introduced differences in peak frequencies between the two electrodes, but post-hoc analyses showed that these differences were not practically meaningful (e.g. C4 during BLO greater than C3 during BLC). Meanwhile, peak frequencies of each electrode did not differ from each other during BLC ($t = -.85$; $p = .41$), BLO ($t = 1.30$; $p = .22$), or OKS ($t = 1.41$; $p = .18$), indicating that the modulations in peak frequency occurred in parallel at both electrodes.

4. Discussion

We showed that performing dynamic handgrip during visual OKS increases occipital upper-alpha, a hallmark of cortical inhibition, even during constant visual stimulation and nystagmus. Dynamic handgrip during OKS also produced the expected bilateral alpha reduction over motor areas, reflecting motor activation and confirming the reliability of the EEG measurement during nystagmus. Contrary to our expectation, the OKN slow-phase velocity increased rather than

decreased during simultaneous dynamic handgrip with OKS compared to OKS alone, but only during left dynamic handgrip. When OKS was presented without dynamic handgrip, a bilateral increase in upper-alpha amplitude was observed over motor areas, supporting that inhibition between the visual and motor systems is mutual. Indeed, simple eye opening already produced a significant shift in motor peak frequency towards upper-alpha which then increased amplitude when OKS was introduced. This suggests that the amount of motor inhibition depends on the amount of visual input. These results extend previous EEG studies that have shown inhibition of the motor system over the visual system and vice versa, also demonstrating that these inhibitory interactions hold when both systems are simultaneously and continuously engaged.

4.1 EEG reliability during nystagmus

A necessary first point to address regards the reliability of EEG assessment during nystagmus. To validate this, we tested whether dynamic handgrip during OKS could reproduce the robust bilateral motor alpha amplitude reduction (cortical activation) classically found during handgrip and other hand movements (Cross-Villasana et al., 2016, Deiber et al., 2001, Gerloff et al., 1998, Pfurtscheller and Lopes da Silva, 1999). When comparing handgrip-OKS against OKS alone, this observation was indeed replicated. This shows that any artefact produced by nystagmus over the EEG need not obscure the alpha-band modulations induced by handgrip. The EEG was refined by the use of ICA to subtract the nystagmus artefact (Bell and Sejnowski, 1995, Makeig et al., 1995) and Surface Laplacian to reduce volume conduction (Kayser and Tenke, 2015, Tenke and Kayser, 2005). In this way, it was also possible to reproduce the activation of the visual cortex when OKS is presented alone, reflected by an alpha-amplitude decrease, as in previous OKS-EEG studies (Gulyás et al., 2007, Magnusson et al., 1985) and fMRI studies (Becker-Bense et al., 2006, Bense et al., 2001, Dieterich et al., 2003, Kikuchi et al., 2009). With the reliability of EEG confirmed, we proceeded to analyse the inhibitory interactions between the visual and motor systems, their effect on nystagmus, and motor inhibitory effects produced by OKS.

4.2 Motor inhibitory influence over the visual cortex and effect on OKN

During simultaneous handgrip-OKS, apart from motor activation, we detected the occipital alpha enhancement known to be produced by isolated hand movements (Cross-Villasana et al., 2018, Deiber et al., 2001, Pfurtscheller and Lopes da Silva, 1999). This implies inhibitory influence over the visual cortex, even as it was continuously stimulated by the optokinetic visual display. This proposal is supported by the suggested inhibitory function of alpha band oscillations (Bazanova and Vernon, 2014, Jensen and Mazaheri, 2010, Klimesch et al., 2007, Pineda, 2005, Romei et al., 2008, Sauseng et al., 2009), especially in the upper-alpha sub-region (Hummel et al., 2002, Klimesch et al., 2007, Pfurtscheller and Lopes da Silva, 1999, Zarkowski et al., 2006). While the posterior alpha enhancement during simultaneous OKS and dynamic handgrip resembles that of isolated dynamic handgrip (Cross-Villasana et al., 2016), in the context of OKS it implies that visual cortical activation was interfered with by the repetitive handgrip movement. For that reason, this observation complements previous electrophysiological evidence where one active thalamocortical stream can be interrupted by the activation of a second stream (Crabtree and Isaac, 2002, Zikopoulos and Barbas, 2007), within our current case, the visual stream being interrupted by the motor stream. In the same way, it confirms that these inhibitory interactions, likely mediated initially at the thalamus, can be observed with scalp EEG as an increase in alpha power (Hughes and Crunelli, 2005, Larson et al., 1998, Vijayan and Kopell, 2012) reflecting the interfered thalamocortical stream (Pfurtscheller and Lopes da Silva, 1999, Steriade, 2000, Sterman, 1996).

Converging evidence supports the idea that motor activation can interfere with visual processing. For example, the latency of saccade execution towards a target is slower whenever it is accompanied by a hand movement, suggesting that the hand movement interfered with the visual processes that lead to the saccade (Sailer et al., 2015). Research in cat and monkey has shown that periods of increased visual attention are accompanied by motor inhibition, muscle tone reduction

and motor cortical down-regulation, presumably to reduce motor interference (Rougeul et al., 1979, Sterman, 1996). In humans, O'Muircheartaigh et al. (2015) observed in a large fMRI sample that resting activity levels of the visual and motor thalamocortical streams are strongly anti-correlated. When Kober et al. (2015) trained participants to enhance the EEG sensorimotor-rhythm (12-15 Hz) by reducing their resting muscular activation, they observed improved performance and enhanced event-related potentials in a visual short-term memory task. After the training, Kober et al. also observed reduced resting EEG functional connectivity between motor and parieto-occipital areas. Together, those findings suggest that reduced interference between motor and visual areas lead to improved visual stimulus processing and task performance (Kober et al., 2015). In contrast, we here produced a deliberate interference of the visual system by the motor system.

Together with alpha enhancement, dynamic-handgrip also increased OKN slow phase velocity, although only with the left hand. This contrasts with previous observations where spontaneous alpha bursts during OKN co-occurred with reductions in nystagmus slow-phase velocity (Magnusson et al., 1985). We propose that in the case of Magnusson et al. these spontaneous alpha bursts most likely reflect a temporary drift of attention or alertness, while in our case they result from the interference of deliberate motor activation during engaged visual processing. Feasibly (although speculatively), perceptual processing of the OKS was disrupted and the OKN slow-phase velocity increased as an adjustment to relocate the moving bars. Nonetheless, it remains a question why this effect was only significant for the left hand. As tentative explanation, interhemispheric competition may have affected the compensatory increase in slow-phase velocity. The higher vestibular system, dominant in the right hemisphere in right-handers (Dieterich and Brandt, 2018), integrates and adjusts various sensory signals, including vision, in order to maintain balance (Dieterich and Brandt, 2015). It is hence possible that the left hemispheric motor dominance associated with right hand exercise interfered with the vestibular system in the right hemisphere (Arshad, 2017, Bloom and Hynd, 2005), affecting the processes that lead to the OKN adjustment after the visual cortex was disrupted. Further work will be necessary to investigate this hypothesis.

4.3 Inhibitory influence over the motor cortex with increasing visual input

Eye opening produced a faster peak frequency over the motor region, on average 1 Hz faster than the eyes closed condition, within the upper-alpha range. The presentation of OKS alone further increased the amplitude of this new frequency peak, apart from eliciting the expected visual activation. This supports that OKS produced the simultaneous inhibition of the motor system, and activation of the visual system, in accordance with previous OKS-fMRI observations (Becker-Bense et al., 2006), and with EEG studies using other kinds of visual stimuli (Brechet and Lecasble, 1965, Koshino and Niedermeyer, 1975, Pfurtscheller and Lopes da Silva, 1999). Considering that upper-alpha is especially associated with inhibitory phenomena (Hummel et al., 2002, Klimesch et al., 2007, Pfurtscheller and Lopes da Silva, 1999, Zarkowski et al., 2006), it can be proposed that increasing visual input, from closed eyes, to eye opening, to visual stimulation, produces progressively greater inhibition of the motor cortex. This argument is supported by research using transcranial magnetic stimulation (TMS), where changes in the state of the visual cortex affect motor-cortical excitability. For example, a TMS pulse to the visual cortex reduces the motor-evoked-potential produced by a second pulse to the motor cortex (Strigaro et al., 2015). Furthermore it has been shown that simply opening the eyes reduces motor excitability, while putting on a blind-fold increases it (Leon-Sarmiento et al., 2005, Strigaro et al., 2015). Overall, these parallel findings in EEG, fMRI and TMS support that the current upper-alpha enhancement during OKS does represent a state of motor down-regulation produced by visual activity.

4.4 Implications for clinical vestibular research

Whole scalp EEG holds great potential as a valuable tool in research fields involving nystagmus, such as vestibular research, since it can compensate for the lack of temporal resolution in other techniques currently used in the field (Lopez and Blanke, 2011). Our whole-scalp recording

during OKS supports the use of EEG when nystagmus artefacts are unavoidable. Eye-movement artefacts can be effectively dealt with through current techniques and technologies, allowing new realms of EEG analysis (e.g. Cross-Villasana et al., 2018, Delorme et al., 2012, Delorme et al., 2007). In our current study, these techniques were the ICA and Surface Laplacian. The use of electro-oculography for precise detection of nystagmus, and a large density of electrodes for better spatial filtering is recommended to reliably isolate the signal of interest through these techniques.

A better understanding of multisensory interactions could help in the development of rehabilitation strategies that rely on multisensory input for treating vestibular disorders (Cousins et al., 2014, Karnath and Dieterich, 2006). For example, in the rehabilitation of visually induced dizziness or functional dizziness, down-regulating the visual cortex during OKS exposure through handgrip exercise could accelerate in the desensitization to visual motion (Cousins et al., 2014, Guerraz et al., 2001), and help retrain reliance on the vestibular system for keeping balance (Cousins et al., 2014).

4.5 Limitations

The current experimental design was fashioned after fMRI OKS studies (Becker-Bense et al., 2006, Bense et al., 2001, Dieterich et al., 2003, Kikuchi et al., 2009) to prove the feasibility of whole-scalp EEG measurement during nystagmus and extend the previous EEG observations on OKS (Gulyás et al., 2007, Magnusson et al., 1985) to the motor cortex. However, it did not allow for the analysis of all scalp electrodes to explore other cortical regions. Given the long-running 45 sec blocks and the computational demands of the wavelet analysis, it was necessary to restrict analysis to those electrodes included in the experimental hypothesis. Meanwhile, FFT data was not feasible for statistical analysis since it misses the dynamic modulations between visual and motor cortices occurring along the 45 sec blocks. The wavelet parameters, tailored for frequency precision over time precision, did not allow investigating the time-span of the inhibitory pulses produced over the visual cortex after each handgrip, or those over the motor cortex during OKS. Having confirmed that the inhibition is reflected by the upper-alpha band, future studies can tune wavelet analysis to be more time-sensitive and in this way investigate the time course of inhibitory pulses. With these same limitations, we were not able to explain why the slow-phase velocity of nystagmus was only increased during left handgrip, and not right handgrip: this could be clarified by modulations in other brain regions not included in current analysis. A future event-related design that allows tracking the events in the brain after each handgrip during nystagmus may help explain this phenomena.

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Declaration of competing interest

None of the authors have potential conflicts of interest to be disclosed.

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