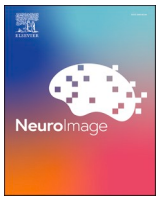
NeuroImage 337 (2026) 122025

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



Unveiling top-down modulation of Hand blink reflex: The frontoparietal network of defensive peripersonal space

Monica Biggio [a], Costanza Iester [b], Ambra Bisio [b], Simone Cutini [c], Sabrina Brigadoi [c], Laura Bonzano [a,d,**], Marco Bove [b,d,*]

[a] Department of Neuroscience, Rehabilitation, Ophthalmology, Genetics, Maternal and Child Health, DINOGMI, University of Genoa, Genoa, Italy
[b] Department of Experimental Medicine, DIMES, Section of Human Physiology, University of Genoa, Genova, Italy
[c] Department of Developmental Psychology, University of Padova, Padova, Italy
[d] IRCCS Azienda Ospedaliera Metropolitana, Genoa, Italy

ARTICLE INFO

Keywords:
fNIRS
Hand blink reflex
Defensive peripersonal space
Parietal cortex
Frontal cortex
Somatosensory cortex
Electrical stimulation

ABSTRACT

The Hand Blink Reflex (HBR) is a subcortical reflex response influenced by limb position in relation to the Defensive Peripersonal Space (DPPS) of the face.

We investigated its cortical correlates with functional Near-Infrared Spectroscopy (fNIRS) by measuring cortical hemodynamic activity before and after evoking the HBR in NEAR (hand close to the face) and FAR (hand far from the face) positions, with the aim to explore whether cortical activity associated with arm positioning predicted HBR modulation. We hypothesized that HBR would elicit activation of the frontoparietal network involved in DPPS encoding.

PRE_STIMULUS analysis revealed significant activity in primary somatosensory cortex (Brodmann area (BA) 3) and posterior parietal cortex (BA40) modulated by arm position. Enhanced activity in NEAR position might suggest increased salience of potential threats based on the integration of body-and-spatial information. BA3 and BA40 activity showed a significant correlation ($r = 0.60$; $p = 0.002$), indicating a functional relationship in encoding body representation with respect to the spatial context. POST_STIMULUS analysis revealed sustained BA3 activation and a decreased activity in the right inferior frontal cortex (BA44). Further, a negative correlation was found between BA44 activity and HBR duration ($r = -0.36$; $p = 0.033$), supporting a mechanism whereby the threat evaluation affects inhibitory control, facilitating defensive responses.

These findings show that top-down modulation of HBR begins before stimulus onset with the activation of a frontoparietal network, integrating sensory and spatial cues and influencing subcortical circuits, adapting the defensive behavior as a function of the body segments position.

1. Introduction

The somatosensory blink reflex is a bilateral protective eye-closure reflex triggered by the electrical stimulation of upper and lower limb nerves (Miwa et al., 1998; Versace et al., 2021; Kofler et al., 2024). The largest response of this reflex occurs when the stimulation is applied to the median nerve at the wrist level: the Hand Blink Reflex (HBR) (Sambo et al., 2012b; Kofler et al., 2024). Among the possible explanations for the larger magnitude of the blink reflex elicited by median nerve stimulation there is the greater proximity of the upper limb to the face compared to the lower limb. In fact, HBR is higher when the stimulated arm is positioned close to the face compared to a more distant position (Sambo et al., 2012b; Fossataro et al., 2016b; Bisio et al., 2017). This finding can be seen as a neurophysiological correlate of the defensive peripersonal space (Defensive PPS or DPPS), a "virtual dynamic bubble" surrounding a person, particularly around the face, where individuals are more vigilant and ready to respond to potentially threatening stimuli (de Vignemont and Iannetti, 2015). Experimental evidence suggests that brainstem circuits mediating the HBR are subject to tonic and selective top-down modulation by higher-order cortical tuning and that its

* Corresponding author at: University of Genoa, Department of Experimental Medicine - Section of Human Physiology, Viale Benedetto XV 3, 16132, Genoa, Italy.
** Corresponding author at: University of Genoa, Department of Neuroscience, Rehabilitation, Ophthalmology, Genetics, Maternal and Child Health, Largo Paolo Daneo, 3 16132, Genoa, Italy.
E-mail addresses: laura.bonzano@unige.it (L. Bonzano), marco.bove@unige.it (M. Bove).

https://doi.org/10.1016/j.neuroimage.2026.122025
Received 29 December 2025; Received in revised form 13 May 2026; Accepted 1 June 2026
Available online 2 June 2026

amplitude is strongly dependent on contextual threat evaluations (Sambo et al., 2012b; Kofler et al., 2024). Sambo and colleagues suggested that, in humans, HBR modulation involves cortical areas similar to those responsible for threat processing in monkeys, namely the ventral intraparietal area and the polysensory zone in the precentral gyrus. Electrical stimulation of these areas induces defensive responses in monkeys, such as squinting and protecting the face with the limbs (Graziano et al., 2002; Graziano and Cooke, 2006). An anatomical correspondence in humans may refer to a frontoparietal network including the dorsal and ventral premotor cortices and the intraparietal sulcus (di Pellegrino and Làdavas, 2014).

The hypothesis of a top-down modulation of the HBR has been investigated in several studies, since it depends on the arm position as well as other factors. Our group has shown that not only the static limb position but also the programmed limb movement direction contributes to influence HBR amplitude (Bisio et al., 2017). This finding suggests that the expected hand position is relevant for risk assessment, likely modulating DPPS representation. We also showed that previous consolidated sensorimotor experience, such as specific body postures learnt during sports activities, can influence HBR amplitude modulation (Biggio et al., 2019), demonstrating the important role of the cerebral cortex in dynamically modulating the HBR. However, to our knowledge, no studies so far have investigated directly the cortical correlates of the HBR.

The current gold standard for brain imaging is functional MRI, but in the scanner the freedom of movement of participants is limited and this can affect the movement itself (Bisio et al., 2016). One feasible way to address this issue is to use functional Near-Infrared Spectroscopy (fNIRS), a neuroimaging technique that uses near-infrared light to measure changes of the concentration of oxygenated hemoglobin (O_2Hb) and deoxygenated hemoglobin (HHb) in the human cerebral cortex (Ayaz et al., 2022). Indeed, fNIRS imposes negligible constraints on participants (in both physical and motor terms), allowing them to move freely while providing an ecologically valid experimental setting (Cutini and Brigadoi, 2014).

Here, we sought to investigate the cortical substrates of the HBR using fNIRS. The paradigm introduced by Sambo and colleagues (Sambo et al., 2012b) was used here to answer to two intertwined questions: (i) Can the cortical activity related to upper limb positioning before stimulation predict HBR?; (ii) Can median nerve stimulation, triggering HBR, evoke the activation of the cortical frontoparietal network involved in encoding defensive peripersonal space?

To this aim, we recorded the hemodynamic cortical activity of 28 healthy participants ten seconds before and after the electrical median nerve stimulation inducing the HBR, while participants held their right hand at two different target positions relative to the face (near and far).

2. Materials and methods

Participants. Inclusion criteria required right-hand dominance, assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), and no history of neurological disorders or orthopedic conditions affecting the dominant hand.

Thirty right-handed healthy participants, who were naïve to the purpose of the study, were recruited and underwent a non-invasive electromyography (EMG) session, while their cortical activity was recorded using fNIRS. Due to technical issues that arose during the data acquisition process, two participants were excluded from the subsequent analysis. Consequently, a total of twenty-eight participants (15 females and 13 males, mean age $\pm$ SD $= 23.04 \pm 2.94$ years) were included in the analysis.

Participants gave written informed consent before taking part in the study. The study was approved by the local ethics committee (Comitato Etico per la Ricerca di AteneoCERA, N. 2023/64 del Comitato Etico per la Ricerca di Ateneo) and was conducted in accordance with the Declaration of Helsinki.

2.1. Experimental set up

Neurophysiological assessment. The HBR response was elicited by administering a transcutaneous electrical stimulus to the median nerve at the right wrist, using a surface bipolar electrode attached with a velcro strap and connected to a Digitimer constant current stimulator (DS7AH HV, Digitimer Ltd, UK). Stimulus duration was 200 μs and its intensity was adjusted to elicit in each participant clear HBR responses (mean stimulus intensity $\pm$ SD $= 6.54 \pm 2.74$ mA). None of the participants reported painful sensations.

EMG activity was recorded by means of two MP100 BIOPAC EMG channels from the orbicularis oculi muscles bilaterally, using two pairs of bipolar surface electrodes with the active electrode over the mid lower eyelid and the reference electrode laterally to the outer canthus. Signals were amplified and digitized at 1 kHz (BIOPAC Systems, Inc., Goleta, CA, USA).

Cortical activity assessment. fNIRS data were acquired with a continuous-wave, portable, multichannel NIRS system (NIRSport 2, NIRx Medical Technologies, Berlin, Germany), consisting of 16 LED illumination sources and 16 active detection sensors operating at two continuous wavelengths of near-infrared light (760 nm and 850 nm) to detect changes in concentration of O2Hb and HHb. Optodes were arranged on a soft black tissue cap (EasyCap, Germany) on the participants' head to cover prefrontal, premotor, motor, sensory and parietal brain areas.

The participant's head circumference was measured to select the appropriate cap size. Correct optode placement was ensured using an fNIRS cap based on the international 10–10 EEG system. The vertex (Cz in EEG references) was located at the midpoint between the nasion, inion, and bilateral tragus points for accurate positioning. The array consisted of 37 standard channels (3 cm). The anatomical localization of the channels was determined using the Brodmann atlas implemented in the fNIRS Optodes' Location Decider (fOLD) toolbox (Zimeo Morais et al., 2018), with the area showing the highest likelihood selected in the case of multiple associations. Consequently, channels belonging to the same hemisphere and Brodmann areas (BA) were averaged, resulting in 18 regions of interest (ROIs: BA3, BA4, BA6, BA7, BA8, BA9, BA39, BA40, and BA44 for both the left and right hemispheres – see Table 1 for the list of standard channels, their MNI coordinates, and the associated BAs). Additionally, 8 short-separation (SS) channels (8 mm) were used to measure solely the extracerebral signals.

2.2. Experimental procedure

HBR was evoked by administering transcutaneous electrical stimulation to the right median nerve of the wrist in the two target positions with respect to the face: i.e., when the elbow angle was: 10° less than the maximal arm extension (FAR position) and 10° more than the maximal elbow flexion (NEAR position). Participants were seated on a chair with their right elbow at the edge of the table, resting on a support: the position allowed the right hand to be in front of the ipsilateral eye in the NEAR position, without contact, and to be able to take the FAR position correctly, slightly elevated above the plane. Throughout the experiment, participants were instructed to keep the non-stimulated arm relaxed in their lap.

Fifteen HBR responses were recorded from both positions, for a total of thirty trials. We also introduced 5 catch trials per condition to reduce expectation, in which participants were asked to adopt the NEAR or FAR position, but no electrical stimulation was administered. Throughout the duration of the experiment participants were asked to wear earplugs to prevent receiving auditory cues from the stimulation, and to maintain their gaze on a fixation cross displayed on the wall in front of them.

Simultaneously with the neurophysiological assessment, we performed the fNIRS acquisition.

A custom Matlab (MATLAB R2021a, MathWorks) script was written to synchronize the fNIRS recording with the electrical stimulation: the

Table 1
List of standard channels, including corresponding optode (source and detector) locations based on the international 10–10 EEG system, MNI coordinates, associated BAs, and hemisphere.

Channel	Source	Detector	x	y	Z	BA	Hemisphere
1	CP2	C2	28	−36	71	3	right
2	C4	C2	42	−21	62	4	right
3	FC2	FC4	39	12	54	6	right
4	FC2	C2	27	−4	68	6	right
5	C4	FC4	52	−4	48	6	right
6	CP2	P2	25	−62	63	7	right
7	P4	P2	33	−74	48	7	right
8	FC2	F2	24	26	55	8	right
9	Fz	AFz	2	50	39	9	right
10	AF4	F2	22	52	33	9	right
11	F4	F2	30	40	41	9	right
12	Fz	F2	10	41	50	9	right
13	P4	CP4	46	−62	47	39	right
14	P4	P6	47	−72	30	39	right
15	CP6	P6	58	−58	22	39	right
16	C4	CP4	53	−35	52	40	right
17	CP2	CP4	39	−49	60	40	right
18	CP6	CP4	58	−48	38	40	right
19	F4	FC4	44	25	40	44	right
20	CP1	C1	−27	−36	71	3	left
21	C3	C1	−42	−20	62	4	left
22	FC1	FC3	−38	12	55	6	left
23	FC1	C1	−26	−5	68	6	left
24	C3	FC3	−50	−3	50	6	left
25	CP1	P1	−24	−62	62	7	left
26	P3	P1	−32	−73	47	7	left
27	FC1	F1	−23	26	56	8	left
28	AF3	F1	−23	52	32	9	left
29	Fz	F1	−9	41	50	9	left
30	F3	F1	−31	39	41	9	left
31	P3	CP3	−46	−61	46	39	left
32	P3	P5	−46	−72	30	39	left
33	CP5	P5	−57	−57	21	39	left
34	C3	CP3	−52	−34	52	40	left
35	CP1	CP3	−39	−48	60	40	left
36	CP5	CP3	−57	−48	38	40	left
37	F3	FC3	−45	25	41	44	left

script allowed to pseudo-randomize trial order, and to simultaneously trigger the electrical stimulator through a National Instruments (NI USB-6009) device and send markers of the different conditions to the Aurora fNIRS software (version 2020.3, NIRx Medical Technologies, Berlin, Germany) through the "Lab Streaming Layer" (LSL - https://github.com/sccn/labstreaminglayer) library. Trials were conducted as follows: the participant received instructions and assumed the designated position (FAR or NEAR) to be maintained throughout the trial, than held still for 10 s to avoid including any hemodynamic changes caused by movement in the next phase; the experimenter checked the position and started the script, which immediately sent a marker to Aurora; then, after a 10-second (+ 1–3 s jitter) period, the script triggered the electrical stimulator to evoke HBR and sent another marker to Aurora. Participants were instructed to maintain the arm position for 10 s (+ 1–3 s jitter) after stimulation. We recorded the cortical activity immediately preceding the electrical stimulation (PRE_STIMULUS) and immediately after the electrical stimulation, containing the HBR response (POST_STIMULUS) in the two arm positions, for a total of four conditions (see Fig. 1). The script was designed to maintain an inter-stimulus interval of at least 30 s between stimulations to prevent HBR habituation (Bisio et al., 2017)

All experiments were conducted in a single session, with an approximate duration of 30 min.

2.3. Data analysis

HBR analysis. EMG signals were processed using custom MatLab software. HBR signals from each participant were filtered and rectified.

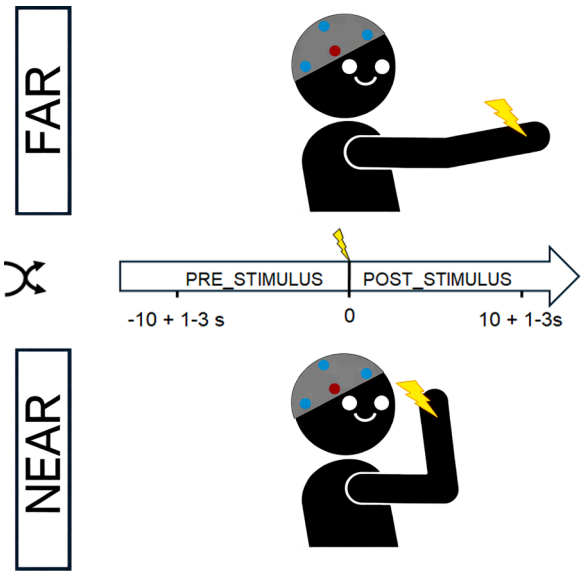


Fig. 1. Experimental paradigm. Figure shows the two target positions assumed randomly by the participants during the experiment (above: FAR position; below: NEAR position) while undergoing fNIRS recording. Participants kept their arm in the target positions for 10-second (+ 1–3 s jitter) before the electrical stimulation at 0 (PRE_STIMULUS) and for 10-second (+ 1–3 s jitter) after the electrical stimulation (POST_STIMULUS).

Trials with an abnormal EMG activity preceding the HBR response were discarded, for a total of <2% of the total trials. The software automatically analyzed each EMG trace in a 130 ms-time interval from the stimulus onset that contained the participant's blink. Then responses were averaged separately for each condition and for each participant. We measured three outcome parameters: the area of the reflex, the latency and the duration. The area under the curve (AUC, mV*ms) of HBR averaged waveform was calculated over the entire 130 ms of the trace. The latency (ms) was defined as the onset of the reflex response, while the duration (ms) was calculated as the difference between the reflex offset and its onset (Bisio et al., 2017; Biggio et al., 2022).

fNIRS analysis. The pre-processing of fNIRS data was carried out using MATLAB with in house scripts, incorporating several functions from the Homer3 NIRS processing package (Huppert et al., 2009). For each participant, all channels with a low signal-to-noise ratio were discarded (SNR<2). Then, the intensity data of the remaining channels were converted to optical density changes. Motion artifacts were corrected by a wavelet (iqr=0.5) (Molavi and Dumont, 2012) motion correction technique.

A band-pass filter (0.01–3 Hz) was applied to remove slow drifts, and very high frequency oscillations. An age-dependent differential path-length factor was computed for each participant (Scholkmann and Wolf, 2013) then the O_2Hb and HHb concentration changes were computed through the modified Beer-Lambert law (Delpy et al., 1988). To calculate the mean hemodynamic response function (HRF) for each condition, participant, and channel, a General Linear Model (GLM) was applied. Iterative weighted least squares were used to solve the GLM (Barker et al., 2013). A set of a consecutive sequence of gaussian functions with a spacing and standard deviation of 2 s was used as temporal basis functions for HRF. The interval for the block average was −2 to 10 s from the trial identification marker. For each standard channel, as an additional regressor in the GLM, the most correlated short-separation channel was used to remove physiological noise.

Then, HRFs of channels belonging to the same BA and hemisphere were averaged obtaining the HRFs of 18 regions of interest (See Table1 and Fig. 3).

2.4. Statistical analysis

Normality of data distribution was checked for all variables with Shapiro-Wilk tests; then, parametric or non-parametric tests were applied accordingly. Data is reported as mean ± standard error of the mean.

HBR analysis. For the POST_STIMULUS conditions, AUC values, blink duration and latency were evaluated with a repeated-measure ANOVA with EYE (2 levels: ipsilateral and controlateral) and POSITION (2 levels: FAR and NEAR) as within-subject factors. Newmann-Keuls post hoc analysis was used to interpret significant interactions.

fNIRS analysis. To explore the cortical activity preceding the electrical stimulation (PRE_STIMULUS condition), O_2Hb concentration changes were analyzed and the differences between the two arm positions were tested using a repeated-measure ANOVA with POSITION (2 levels: FAR and NEAR), BA (9 levels: BA3, BA4, BA6, BA7, BA8, BA9, BA39, BA40 and BA44) and HEMISPHERE (2 levels: L and R) as within-subject factors. A repeated-measures ANOVA with the same factors was conducted to reveal the differences in cortical activity between positions and hemispheres in response to electrical stimulation (POST_STIMULUS condition).

The same analyses were also conducted for the HHb concentration changes. Newmann-Keuls post-hoc analysis was used to interpret significant interactions.

Correlations. To assess relationships between behavioral response and cortical activity, HBR latency, duration and AUC were correlated with O_2Hb concentration changes, separately for the PRE_STIMULUS and POST_STIMULUS conditions, in the BAs that showed statistical significance in the previous analysis. Specifically, Spearman's rank correlation was computed for AUC and duration, due to their non-normal distribution when data from the hand positions were pooled together, whilst Pearson's correlation was applied for latency. In addition, Pearson's correlation was used to assess the relationship between the changes in O_2Hb concentration in the active BAs during each phase separately, as well as between the changes in O_2Hb concentration in the same BA when active in both phases.

3. Results

3.1. HBR

Statistical analysis of the average amplitudes showed significant effects for both the main factors, i.e., EYE ($F_{(1,27)} = 9.86$, $p = 0.004$) and POSITION ($F_{(1,27)} = 54.43$, $p = 0.001$), and a significant effect for the interaction EYE*POSITION ($F_{(1,27)} = 8.07$, $p = 0.008$). Post-hoc analysis showed that the AUCs recorded from the ipsilateral eye were significantly greater than the ones recorded from controlateral eyes (28.42 ± 2.31 vs. 21.92 ± 1.37 mV*ms; $p = 0.004$), and that blinks recorded in NEAR have significant grater areas than the ones recorded in FAR (31.87 ± 3.49 vs. 20.79 ± 1.97 mV*ms; $p = 0.001$). Also, post-hoc analysis showed that the AUCs in NEAR-ipsilateral eye (34.58 ± 3.71 mV*ms) were significantly greater than all the other conditions (FAR-ipsilateral eye: 22.26 ± 2.30 mV*ms, $p < 0.001$; NEAR-controlateral eye: 25.90 ± 2.16 mV*ms, $p < 0.001$; FAR-controlateral eye: 17.93 ± 1.35 mV*ms, $p < 0.001$). Furthermore, AUCs in NEAR-controlateral eye were significantly higher than FAR-ipsilateral ($p < 0.05$) and FAR-controlateral ($p < 0.001$). At last, the AUCs evoked in the ipsilateral eye in FAR condition were significantly higher than the controlateral eye in the same position

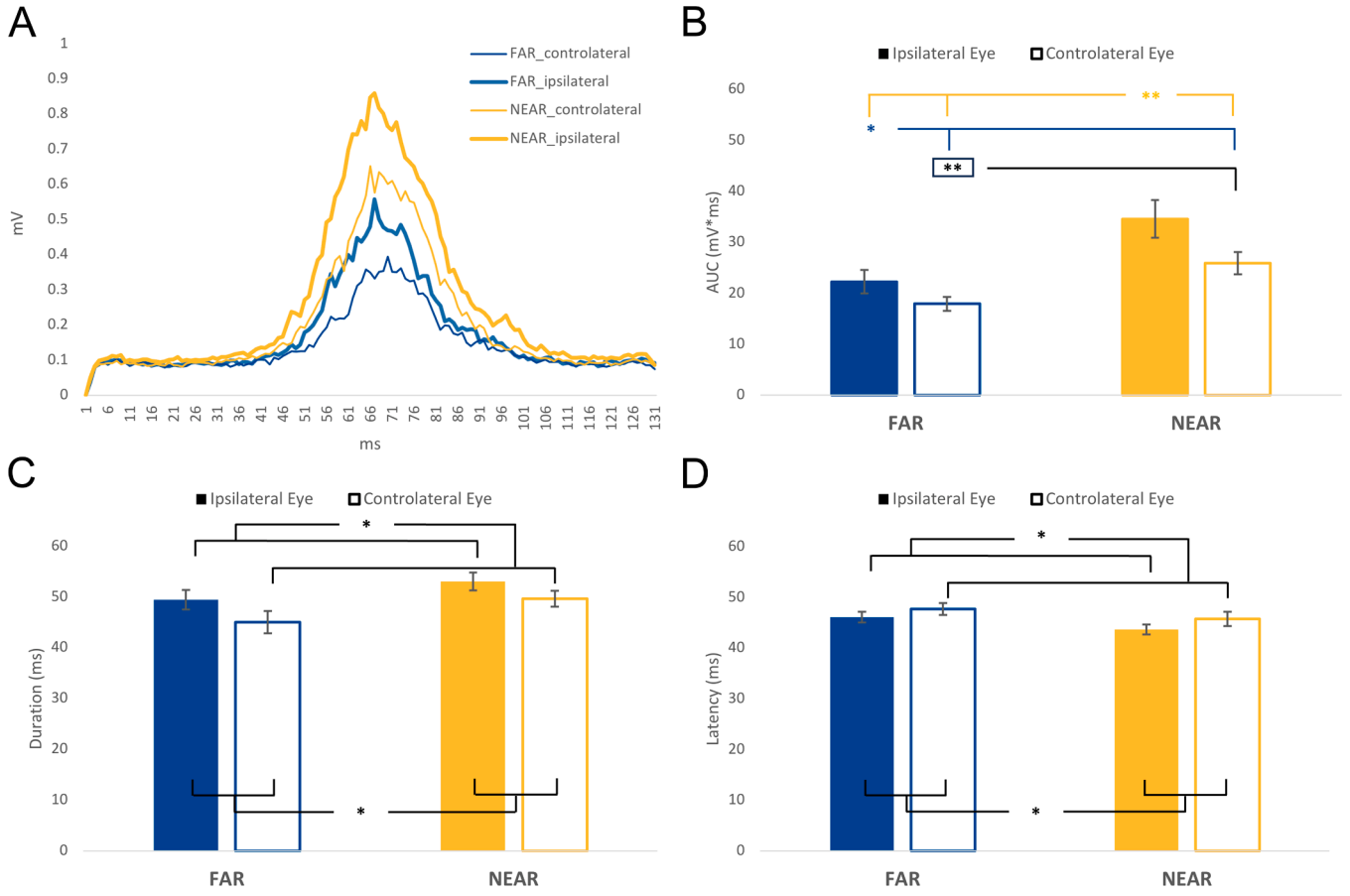


Fig. 2. Panel A shows group-average, rectified HBR waveforms. Other panels show group-average HBR parameters: Amplitudes (B), Duration (C) and Latency (D) recorded when the arm was placed in the two target positions (FAR in blue and NEAR in yellow) from the eye ipsilateral to the stimulated hand (full) and contralateral (empty). Error bars indicate standard error. **p < 0.01, *p < 0.05.

($p < 0.001$). Results are shown in Fig. 2.

Statistical analysis of the average duration showed significant effects of EYE ($F_{(1,27)} = 5.21$, $p = 0.031$) and POSITION ($F_{(1,27)} = 5.83$, $p = 0.023$). No significant interaction was found ($p = 0.675$). Post-hoc analysis showed that the durations of the reflex recorded from the ipsilateral eye were significantly greater than the ones recorded from controlateral eye (51.26 ± 1.31 vs. 47.35 ± 1.37 ms; p = 0.031) and that blinks were longer in NEAR than in FAR (51.37 ± 1.30 vs. 47.24 ± 1.68 ms; $p = 0.023$) (Fig. 2C).

Statistical analysis of the average latency showed significant effects of EYE ($F_{(1,27)} = 6.820$, $p = 0.015$) and POSITION ($F_{(1,27)} = 6.798$, $p = 0.015$). No significant differences were found for the interaction ($p = 0.723$). Post-hoc analysis showed that responses recorded from the ipsilateral eye were significantly more rapid than the ones recorded from controlateral eyes (44.91 ± 0.73 vs. 46.77 ± 0.91 ms; $p = 0.015$) and that blink's latencies were shorter in NEAR than in FAR (44.74 ± 1.07 vs. 46.94 ± 0.96 ms; $p = 0.015$) (Fig. 2D).

3.2. fNIRS

3.2.1. PRE_STIMULUS

Exploring differences in O_2Hb concentration changes, a significant main effect of POSITION ($F_{(1,27)} = 5.81$, $p = 0.023$) was found, showing that the overall cortical activity was significantly lower in FAR than in NEAR position (−9.45 ± 2.83 vs. 1.33 ± 3.18 nM). Also, a significant POSITION*BA interaction was observed ($F_{(8216)} = 2.69$, $p = 0.008$). Post-hoc analysis showed that cortical activity in BA3 and BA40 before the stimulation in NEAR position was significantly higher than in FAR position (BA3 NEAR vs BA3 FAR: 11.62 ± 6.00 vs −12.31 ± 5.92 nM, $p = 0.001$; BA40 NEAR vs BA40 FAR: 3.76 ± 3.73 vs −16.47 ± 4.69 nM, $p = 0.017$) (Fig. 4).

Exploring differences in changes in HHb concentration, no significant effects were found.

3.2.2. POST_STIMULUS

Exploring differences in O_2Hb concentration changes, a significant main effect of the BA factor ($F_{(8216)} = 12.67$, $p < 0.001$) was found. Also, significant interactions between POSITION*BA ($F_{(8216)} = 3.48$, $p < 0.001$) and BA*HEMISPHERE ($F_{(8216)} = 2.86$, $p < 0.001$) were observed.

Post-hoc analysis revealed significant different activations among ROIs, three in particular: BA44 (−8.83 ± 4.11 nM) was significantly deactivated with respect to all the other areas (max $p = 0.045$), except for BA39 ($p = 0.059$). BA3 (24.24 ± 5.29 nM) showed significantly higher activity than the other areas (max $p = 0.017$), except for BA4 ($p = 0.50$). BA4 (21.39 ± 4.94 nM) showed significantly higher activity than the other areas (max $p = 0.039$), except for BA6 ($p = 0.053$) and BA7 ($p = 0.057$). Also, BA39 (−0.80 ± 4.12 nM) showed a significantly decreased activity with respect to BA7 (10.65 ± 4.52 nM, $p = 0.036$), BA6 (11.52 ± 4.01 nM, $p = 0.031$) and BA40 (12.62 ± 3.83 nM, $p = 0.020$).

POSITION*BA interaction showed that cortical activity in BA3 was significantly more positive in NEAR position than in FAR position (BA3 NEAR vs BA3 FAR: 32.73 ± 6.31 vs 15.74 ± 7.07 nM, $p = 0.004$), while in BA44 it was significantly more negative in NEAR than in FAR (BA44 NEAR vs BA44 FAR: −14.06 ± 5.04 vs −3.60 ± 5.81 nM, $p = 0.029$). Results are shown in Fig. 5.

Further, the BA*HEMISPHERE interaction showed that cortical activity in the left hemisphere was significantly higher than in the right hemisphere in BA4 (left BA4 vs. right BA4: 30.49 ± 6.19 vs 12.28 ± 5.18 nM, $p < 0.01$).

Exploring differences in changes in HHb concentration, a significant main effect of the BA factor was found ($F_{(8216)} = 10.67$, $p < 0.001$). Also, a significant BA*HEMISPHERE interaction was observed ($F_{(8216)} = 2.41$, $p = 0.016$).

Post-hoc analysis revealed that BA4 (−8.49 ± 1.97 nM) showed a significantly stronger decrease than all the other areas (max $p = 0.003$), except for BA6 (−5.15 ± 1.24 nM, $p = 0.61$) and BA3 (−5.64 ± 1.59 nM, $p = 0.054$). BA6 showed a significant decrease than the others (max $p = 0.035$), except for BA3 ($p = 0.74$) and BA40 (−3.32 ± 1.32 nM, $p =$

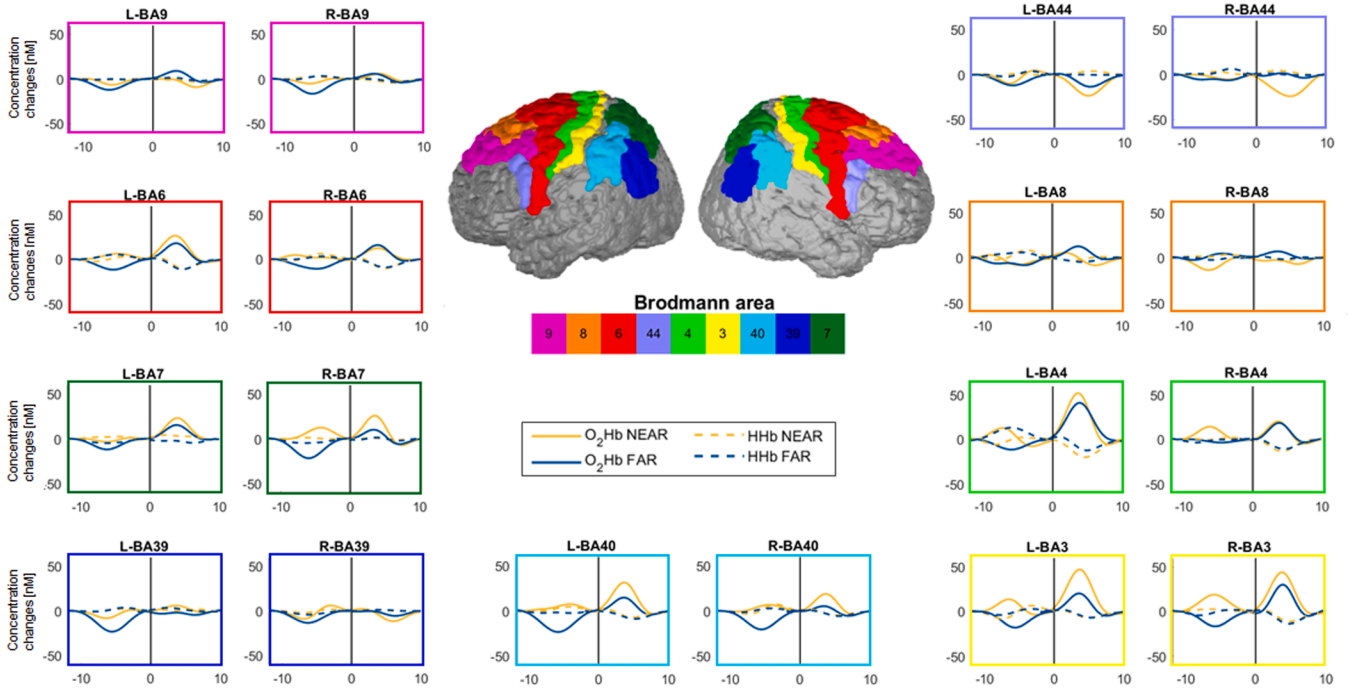


Fig. 3. The boxes show variations in O_2Hb (continuous lines) and HHb (dashed lines) concentrations during PRE_ and POST_STIMULUS phases for NEAR (orange lines) and FAR (blue lines) position. Boxes represent the average of channels corresponding to the same Brodmann areas, associated by color on the brain location in the center, in left (L) and right hemisphere (R). The black vertical line corresponds to the electrical stimulation. The figure is for illustrative purposes only; analyses on the PRE_ and POST_STIMULUS phases were processed separately.

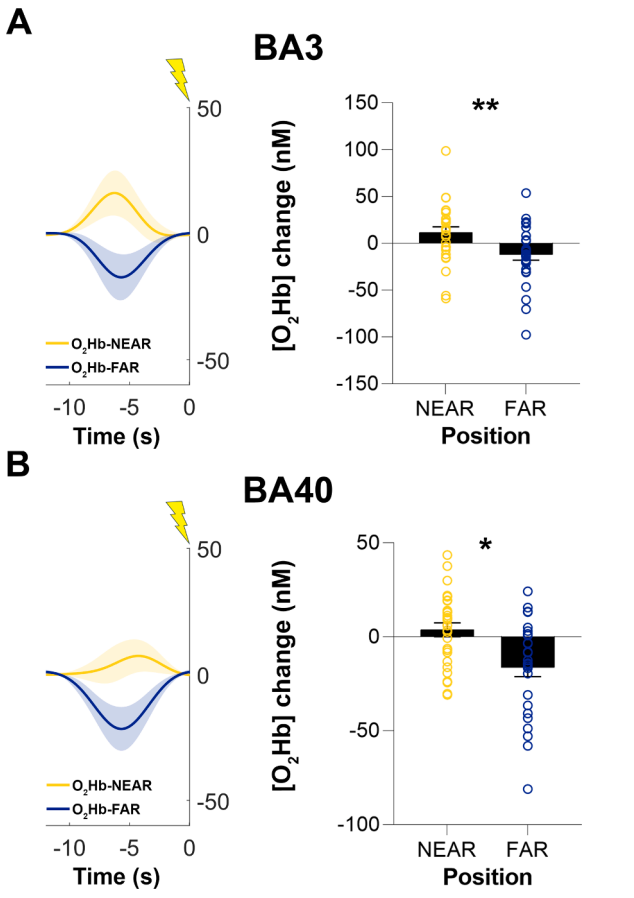


Fig. 4. On the left, variations in Oxy-hemoglobin concentration for the two target positions in BA3 (above – Panel A) and BA40 (below – Panel B) in PRE_STIMULUS condition. The shaded lines represent the standard error. On the right, histograms display the averaged O_2Hb changes, with circles representing individual subject data for the NEAR (yellow) and FAR (blue) positions. * indicates $p < 0.05$, ** indicates $p < 0.01$.

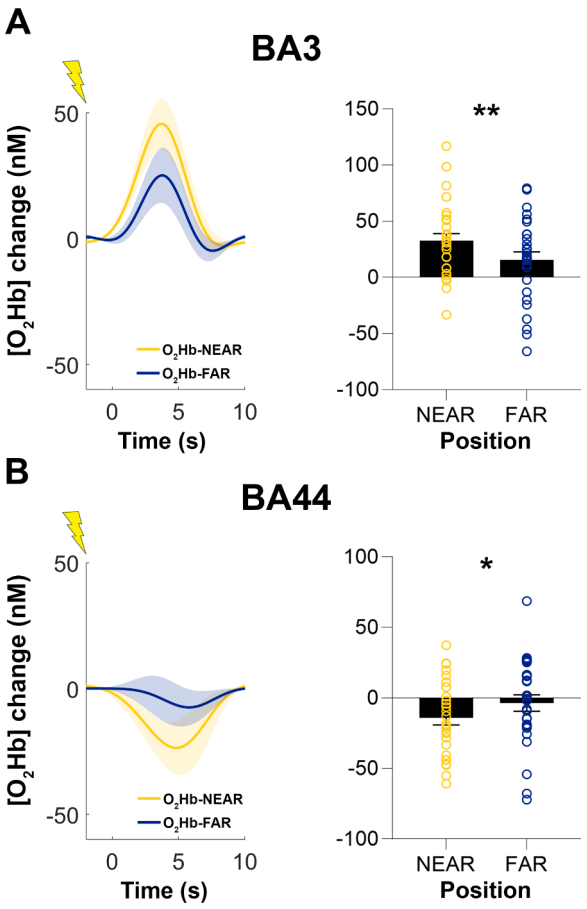


Fig. 5. On the left, variations in Oxy-hemoglobin concentration for the two target positions in BA3 (above – Panel A) and BA44 (below – Panel B) in POST_STIMULUS condition. The shaded lines represent the standard error. Histograms display the averaged O_2Hb changes, with circles representing individual subject data for the NEAR (yellow) and FAR (blue) positions. * indicates $p < 0.05$, ** indicates $p < 0.01$.

0.215). BA3 showed a significant decreased activity than the other (max $p = 0.025$), except for BA40 ($p = 0.257$). BA40 showed a significant higher activity with respect to BA39 (0.92 ± 0.78 nM, $p = 0.033$) and BA44 (1.23 ± 0.93 nM, $p = 0.025$).

The BA*HEMISPHERE interaction showed that the decrease in the left hemisphere was significantly stronger than in the right hemisphere in BA4 (left BA4 vs. right BA4: -11.28 ± 2.50 vs. -5.70 ± 2.29 nM, $p = 0.01$).

3.3. Correlations

Pearson's correlation coefficients were calculated between the averaged HBR latency and the averaged O_2Hb concentration change in left and right BA40 and BA3 in PRE_STIMULUS condition and BA44 and BA3 in POST_STIMULUS condition. Also, Spearman's correlation analyses were performed to assess the correlation of the averaged HBR AUC and duration with O_2Hb in the same BA. False Discovery Rate (FDR) was used to adjust p-values for the multiple comparisons.

A significant correlation was found between HBR latency and O_2Hb in the right BA40 in the PRE_STIMULUS condition ($r(54) = -0.351$, $p = 0.008$, adjusted $= 0.032$).

In the POST_STIMULUS condition, AUC of the blink negatively correlated with the cortical activity of the right BA44 ($r(54) = -0.277$, $p = 0.039$, adjusted $= 0.149$). Also, HBR duration negatively correlated with O_2Hb in the right BA44 ($r(54) = -0.355$, $p = 0.008$, adjusted $= 0.033$).

Pearson's correlation was performed between O_2Hb concentration changes in PRE_STIMULUS between averaged BA3 and averaged BA40 and between averaged BA3 and averaged BA44 in POST_STIMULUS. We found a positive correlation between the areas active in PRE_STIMULUS, meaning BA3 and BA40: $r(54) = 0.60$, $p = 0.001$, adjusted $p = 0.002$. No significant correlation was found in the POST_STIMULUS phase.

Pearson's correlation was performed between O_2Hb concentration changes in averaged BA3 PRE_STIMULUS and BA3 POST_STIMULUS. We found a positive correlation between the BA3 activity in the two phases: $r(54) = 0.29$, $p = 0.028$, adjusted $p = 0.056$.

4. Discussion

In this work, we explored for the first time with fNIRS the cortical control of the Hand Blink Reflex, a defensive response modulated by the arm position with respect to the face. Consistently with previous works, we found an increase in HBR amplitude when the hand was close to the face compared to when it was far from the face (Sambo et al., 2012b; Bisio et al., 2017). Then, we addressed two specific questions: (i) whether cortical activity preceding the stimulation and related to upper limb positioning could predict HBR amplitude, and (ii) whether the stimulation of the median nerve, triggering HBR, could activate cortical frontoparietal networks associated with DPPS.

4.1. Cortical activity in the PRE_STIMULUS phase

Firstly, we focused our attention on the cortical activity recorded 10 s before the electrical stimulation. We observed, in NEAR position, a significant increase of activity in the somatosensory cortex with respect to FAR position, where instead a decrease was present, represented by an inverse hemodynamic response. The difference in BA3 activity observed between the two conditions suggests that the evaluation of position could make one more salient than the other. Indeed, we propose that the stimulus expectancy in NEAR could alert participants, thus increasing the salience of the stimulus based on the prediction of sensory outcome in a potentially more threatening condition.

We also found a significant modulation of BA40 activity as a function of the arm position. BA40 is involved in visuospatial attention processes, with a role of integrating multisensory inputs to represent and continuously update body representation (Matsumiya, 2022; Kamada and Takeuchi, 2023). Further, this area is related to functions of visuo-spatial judgment of body parts (Corradi-Dell'Acqua et al., 2008) with maintenance of an internal stable model of the visual, anatomical and structural information of the body (Tsakiris et al., 2008; Di Vita et al., 2016).

The simultaneous activation of somatosensory and parietal cortical areas, indicated by the significant correlation between them, suggests that the modulation of position-related information salience may depend on their functional interaction. Interestingly, an event-related potential study (Shen et al., 2018) found that presenting somatosensory stimuli across structural boundaries between body parts influenced the N80 response. This response is believed to originate from the contralateral somatosensory cortex, suggesting that structural aspects of body representation impact early somatosensory processing (de Haan and Dijkerman, 2020). Although correlation analysis does not allow us to establish a causal relationship, we tentatively propose that changes in somatosensory cortex activity may be influenced by body representation information originating from the parietal lobe.

Further, right BA40 O_2Hb concentration changes negatively correlated with HBR latency, i.e., the higher the hemodynamic activity in BA40 the faster the blink occurrence. This finding is in line with the notion that a stimulus in NEAR position was evaluated as more threatening, and therefore more salient, than in FAR position.

4.2. Cortical activity in the POST_STIMULUS phase

Participants received a sudden electrical median nerve stimulation in order to evoke HBR with the arm in two target positions. Here, BA3 still showed a significant difference in hemodynamics between the two conditions: a stronger activation in NEAR and a lower one in FAR. Previous research studies dealing with median nerve electrical stimulation show that non-painful tactile stimulations can influence the activity of the somatosensory areas (Backes et al., 2000). Here, we demonstrated that not only the median nerve stimulation features can modulate somatosensory cortex activity, but also the salience attributed to the stimulus. Indeed, we found a significant correlation between activity measured in PRE_ and POST_STIMULUS phases. This could suggest that the activity in the somatosensory cortex after the stimulus is the consequence of the activity present in the same cortical area in the PRE_STIMULUS phase. The latter may be based on a stimulus expectancy process that depends on the evaluation of how potentially threatening the stimulus could be.

On the other hand, we found a significant decrease of the BA44 in NEAR with respect to FAR. This cortical area has a role in inhibitory control (Aron et al., 2004) and reactive inhibition (van Belle et al., 2014), particularly in the right hemisphere. The pattern observed in BA44 could be related to a "brake releasing" mechanism, allowing an increase of the defensive response, based on eye blinking, when the stimulus threat increases. This hypothesis is in line with the negative correlation found between BA44 activity and HBR duration, i.e., the more decreased activity in the BA44, the longer the duration of HBR.

4.3. Cortical frontoparietal network and defensive peripersonal space

With the HBR paradigm, we identified the involvement of a network of cortical areas responsible for the processing of somatosensory inputs at different levels of complexity. In fact, somatosensory information processing refers to multiple intertwined neural networks, such as the frontoparietal circuits responsible for body and PPS representation, and also the ventral attention network which processes the somatosensory inputs. The latter acts as a form of filter on the perceptual and semantic encoding of the stimuli, specifically when working in interaction with the dorsal network (Corbetta et al., 2008; Viviani, 2013).

Attentional networks and PPS representation share an overlapped neural substrate: perceptual and attentional aspects of PPS processing depend mostly on parietal regions, whilst involvement of frontal areas appears to contribute to motor planning and defensive responses in near space (Basile et al., 2024). Such defensive responses may be evolved to prompt immediate withdrawal from noxious stimuli directed to the face and body (Sambo et al., 2012b; Cléry et al., 2015; Vieira et al., 2020). In a recent review, Basile and colleagues (Basile et al., 2024) highlighted that different regions in the frontal and parietal lobes present various circuits underlying the different functions of PPS representation, and that they are tightly interconnected to each other. Specifically, they describe the ventral intraparietal area-ventral caudal premotor cortex (VIP-PMVc) circuit for the space around the arm and head to subserve defensive behavior, corresponding to a BA40–44 circuit (Basile et al., 2024).

In the context of the defensive role of PPS (the "flight zone" (Graziano and Cooke, 2006)), the need for an efficient evaluation of the threat posed by a stimulus becomes evident (Blakemore et al., 2012; Bisio et al., 2017; Biggio et al., 2019). The intensity of the blink reflex might represent the result of a rapid assessment performed by the nervous system to evaluate the potential harm posed by the electrical stimulation to the organism (Sambo et al., 2012b; Kofler et al., 2024), since HBR magnitude reflects the probability of the face being hit by a threat (Bufacchi et al., 2016; Biggio et al., 2019). Furthermore, HBR magnitude is a paradigmatic example of a class of neural and behavioral responses that reflect the value of actions aiming to create or avoid contact between objects and the body (Bufacchi and Iannetti, 2018; Foster et al., 2022).

Up to now, top-down modulation of HBR has been inferred by lesional studies. The reflex was explored in brain-damaged patients, showing that patients with pathological embodiment showed altered NEAR-FAR modulation when the stimulated wrist was the limb of the experimenter pathologically embodied by patients (Fossataro et al., 2016a). Even if the damaged brain regions were heterogeneous across patients, the only common lesional area across patients was the superior longitudinal fasciculus, particularly in the right hemisphere, that authors viewed as responsible of a disconnection between the frontoparietal circuit disrupting bodily ownership and, consequently, failing to modulate HBR correctly.

We can assume that participants are able to anticipate the sensory consequences of different stimuli on the basis of the actual position and prior sensorimotor experiences (Blakemore et al., 2012; Bisio et al., 2017; Biggio et al., 2019; Foster et al., 2022), but also on the basis of cognitive or personality factors that influence these, and that have already been linked to HBR modulation in the literature (Sambo et al., 2012a; Fossataro et al., 2016b; Biggio et al., 2023; Mercante et al., 2024).

Although this is the first study to directly investigate the cortical correlates of HBR, it has some limitations. First, we performed a network-level analysis to identify the cortical regions involved in representing the DPPS; however, the observed correlations do not allow us to infer causal relationships between regions. Further studies are needed to better characterize the temporal dynamics of these areas.

Furthermore, although fNIRS was chosen for its robustness to ocular artifacts and its capability to assess spatially distributed cortical hemodynamic activity, the relatively slow hemodynamic response measured by fNIRS, compared with electrophysiological techniques such as EEG, may constrain the assessment of fast neural dynamics underlying HBR modulation. Additionally, anatomical reconstruction methods for optode placement were not employed; therefore, subtle inter-individual variability in cortical localization cannot be ruled out.

It is also worth noting that several factors have been shown to influence HBR modulation. For example, previous studies have been designed to disentangle visual and tactile contributions (Sambo et al., 2012a; Fossataro et al., 2020), which were not explicitly controlled in the present study. Similarly, expectation was not directly manipulated (Sambo et al., 2012b; Versace et al., 2021; Rossi Sebastiano et al., 2022), although its influence is suggested by the significant differences observed in the PRE_STIMULUS phase between conditions. Overall, this study paves the way for future investigations, from a cortical perspective, into the components that may shape the DPPS network.

Summarizing, the different hemodynamic activities observed in BA3, BA40 and BA44 before and after the stimulation in relation to arm position suggest that HBR top-down modulation begins before the stimulus has been perceived, with hazard assessment linked to contextual information acquired during the limb positioning task. Our findings provide indeed affirmative answers to both of the proposed hypotheses. First, PRE_STIMULUS cortical activity appears to be closely linked with body representation information, indicating that the brain encodes and utilizes spatial information about limb positioning to modulate HBR response. Second, we showed that median nerve stimulation, which triggers HBR, can evoke activation in the cortical frontoparietal network associated with encoding DPPS, suggesting its involvement in enhancing the protective response of blinking based on limb location in space. These findings highlight the role of cortical processes in dynamically modulating defensive behaviors in relation to body representation and spatial awareness.

In conclusion, we believe that our study set, for the first time, the basis for understanding the neural mechanisms underlying the HBR and its modulation. This provides valuable insights into the roles of frontal and parietal areas in sensory processing and attentional modulation of a threatening stimulus within the DPPS. Overall, this study advances our understanding of the cortical processes associated with defensive reflexes and highlights the importance of spatial context in shaping these responses.

Ethical approval

The study was approved by the University Ethics Committee (Comitato Etico per la Ricerca di AteneoCERA, N. 2023/64). The work described has been carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans. All participants provided informed consent to participate in the study.

Data and code availability statement

The data supporting the findings of this study are not publicly available at present due to the terms of the ongoing grant. However, data may be made available upon reasonable request to the corresponding author after the conclusion of the grant period.

CRediT authorship contribution statement

Monica Biggio: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Costanza Iester:** Writing – review & editing, Software, Formal analysis, Data curation. **Ambra Bisio:** Writing – review & editing, Software, Methodology, Formal analysis, Data curation. **Simone Cutini:** Writing – review & editing, Data curation, Conceptualization. **Sabrina Brigadoi:** Writing – review & editing, Formal analysis, Data curation. **Laura Bonzano:** Writing – original draft, Supervision, Project administration, Conceptualization. **Marco Bove:** Writing – original draft, Supervision, Resources, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that there are no relevant financial or non-financial competing interests to report.

Acknowledgments

This work was supported by Italian Multiple Sclerosis Foundation (FISM) Grant 2022/R-Multi/040.

References

Aron, A.R., Robbins, T.W., Poldrack, R.A., 2004. Inhibition and the right inferior frontal cortex. Trends. Cogn. Sci. 8, 170–177.
Ayaz, H., et al., 2022. Optical imaging and spectroscopy for the study of the human brain: status report. Neurophotonics 9, S24001.
Backes, W.H., Mess, W.H., Van Kranen-Mastenbroek, V., Reulen, J.P.H., 2000. Somatosensory cortex responses to median nerve stimulation: fMRI effects of current amplitude and selective attention. Clinic. Neurophysiol. 111, 1738–1744.
Barker, J.W., Aarabi, A., Huppert, T.J., 2013. Autoregressive model based algorithm for correcting motion and serially correlated errors in fNIRS. Biomed. Opt. Express. 4, 1366.
Basile, G.A., Tatti, E., Bertino, S., Milardi, D., Genovese, G., Bruno, A., Muscatello, M.R. A., Ciurleo, R., Cerasa, A., Quartarone, A., Cacciola, A., 2024. Neuroanatomical correlates of peripersonal space: bridging the gap between perception, action, emotion and social cognition. Brain Struct. Funct. 229, 1047–1072.
Biggio, M., Bisio, A., Ruggeri, P., Bove, M., 2019. Defensive peripersonal space is modified by a learnt protective posture. Sci. Rep. 9.
Biggio, M., Caligiore, D., D'Antoni, F., Bove, M., Merone, M., 2022. Machine learning for exploring neurophysiological functionality in multiple sclerosis based on trigeminal and hand blink reflexes. Sci. Rep. 12, 1–10.
Biggio, M., Escelsior, A., Murri, M.B., Trabucco, A., Delfante, F., da Silva, B.P., Bisio, A., Serafini, G., Bove, M., Amore, M., 2023. Surrounded, detached": the relationship between defensive peripersonal space and personality. Front. Psychiatry 14.
Bisio, A., Garbarini, F., Biggio, M., Fossataro, C., Ruggeri, P., Bove, M., 2017. Dynamic shaping of the defensive peripersonal space through predictive motor mechanisms: when the "near" becomes "far. J. Neurosci. 37, 2415–2424, 16. http://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.0371-16.2016.
Bisio, A., Pedullà, L., Bonzano, L., Ruggeri, P., Brichetto, G., Bove, M., 2016. Evaluation of handwriting movement kinematics: from an ecological to a magnetic resonance environment. Front. Hum. Neurosci. 10, 488. https://doi.org/10.3389/fnhum.2016.00488.
Blakemore, S.-J., Wolpert, D.M., Frith, C.D., Sambo, C.F., Liang, M., Cruccu, G., Iannetti, G.D., Haggard, P., Sambo, C.F., Iannetti, G.D., Forster, B., Williams, S.C., Iannetti, G.D., Wolpert, D.M., Ghahramani, Z., Jordan, M.I., Series, N., Sep, N., 2012. Defensive peripersonal space: the blink reflex evoked by hand stimulation is increased when the hand is near the face. J. Neurosci. 33, 14225–14230.
Bufacchi, R.J., Iannetti, G.D., 2018. An action field theory of peripersonal space. Trends. Cogn. Sci. xx, 1–15.
Bufacchi, R.J., Liang, M., Griffin, L.D., Iannetti, G.D., 2016. A geometric model of defensive peripersonal space. J. Neurol. 218–225.
Cléry, J., Guipponi, O., Wardak, C., Ben Hamed, S., 2015. Neuronal bases of peripersonal and extrapersonal spaces, their plasticity and their dynamics: knowns and unknowns. Neuropsychologia 70, 313–326.
Corbetta, M., Patel, G., Shulman, G.L., 2008. The reorienting system of the Human brain: from environment to theory of mind. Neuron 58, 306–324.
Corradi-Dell'Acqua, C., Hesse, M.D., Rumiati, R.I., Fink, G.R., 2008. Where is a nose with respect to a foot? The left posterior parietal cortex processes spatial relationships among body parts. Cerebral Cortex 18, 2879–2890.
Cutini, S., Brigadoi, S., 2014. Unleashing the future potential of functional near-infrared spectroscopy in brain sciences. J. Neurosci. Methods 232, 152–156.
de Haan, E.H.F., Dijkerman, H.C., 2020. Somatosensation in the brain: a theoretical re-evaluation and a new model. Trends. Cogn. Sci. 24, 529–541.
de Vignemont, F., Iannetti, G.D., 2015. How many peripersonal spaces? Neuropsychologia 70, 327–334.
Delpy, D.T., Cope, M., Zee, P V.D., Arridge, S., Wray, S., Wyatt, J., 1988. Estimation of optical pathlength through tissue from direct time of flight measurement. Phys. Med. Biol. 33, 1433–1442.
di Pellegrino, G., Làdavas, E., 2014. Peripersonal space in the brain. Neuropsychologia 66, 126–133.
Di Vita, A., Boccia, M., Palermo, L., Guariglia, C., 2016. To move or not to move, that is the question! body schema and non-action oriented body representations: an fMRI meta-analytic study. Neurosci. Biobehav. Rev. 68, 37–46.

Fossataro, C., Gindri, P., Mezzanato, T., Pia, L., Garbarini, F., 2016a. Bodily ownership modulation in defensive responses: physiological evidence in brain-damaged patients with pathological embodiment of other's body parts. Sci. Rep. 6.
Fossataro, C., Sambo, C.F., Garbarini, F., Iannetti, G.D., 2016b. Interpersonal interactions and empathy modulate perception of threat and defensive responses. Sci. Rep. 6, 19353.
Fossataro, C., Tieri, G., Grollero, D., Bruno, V., Garbarini, F., 2020. Hand blink reflex in virtual reality: the role of vision and proprioception in modulating defensive responses. Euro. J. Neurosci. 51, 937–951.
Foster, C., Sheng, W.A., Heed, T., Ben Hamed, S., 2022. The macaque ventral intraparietal area has expanded into three homologue human parietal areas. Prog. Neurobiol. 209, 102185.
Graziano, M.S., Cooke, D.F., 2006. Parieto-frontal interactions, personal space, and defensive behavior. Neuropsychologia 44, 2621–2635.
Graziano, M.S.A., Taylor, C.S.R., Moore, T., 2002. Complex movements evoked by microstimulation of precentral cortex. Neuron 34, 841–851.
Huppert, T.J., Diamond, S.G., Franceschini, M.A., Boas, D.A., 2009. HomER: a review of time-series analysis methods for near-infrared spectroscopy of the brain. Appl. Opt. 48, D280.
Kamada, H., Takeuchi, N., 2023. Transcranial direct current stimulation over the temporoparietal junction modulates posture control in unfamiliar environments. Brain Sci. 13, 1514.
Kofler, M., Hallett, M., Iannetti, G.D., Versace, V., Ellrich, J., Téllez, M.J., Valls-Solé, J., 2024. The blink reflex and its modulation – Part 1: physiological mechanisms. Clinic. Neurophysiol. 160, 130–152. https://doi.org/10.1016/j.clinph.2023.11.015.
Matsumiya, K., 2022. Multiple representations of the body schema for the same body part. Proc. Natl. Acad. Sci. U S. A 119 (4), e2112318119. https://doi.org/10.1073/pnas.2112318119. Erratum in: Proc Natl Acad Sci U S A. 2022 Mar 15;119(11): e2201624119. doi:10.1073/pnas.2201624119.
Mercante, B., Uccula, A., Secchi, E., Puggioni, G., Loi, N., Enrico, P., Deriu, F., 2024. Hand-blink reflex modulation: the role of primary emotions and attachment dimensions. Psychophysiology 61 (1), e14432. https://doi.org/10.1111/psyp.14432.
Miwa, H., Nohara, C., Hotta, M., Shimo, Y., Amemiya, K., 1998. Somatosensory-evoked blink response: investigation of the physiological mechanism. Brain 121, 281–291.
Molavi, B., Dumont, G.A., 2012. Wavelet-based motion artifact removal for functional near-infrared spectroscopy. Physiol. Meas. 33, 259–270.
Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.
Rossi Sebastiano, A., Ronga, I., Fossataro, C., Galigani, M., Poles, K., Garbarini, F., 2022. Multisensory-driven facilitation within the peripersonal space is modulated by the expectations about stimulus location on the body. Sci. Rep. 12.
Sambo, C.F., Forster, B., Williams, S.C., Iannetti, G.D., 2012a. To blink or not to blink: fine cognitive tuning of the defensive peripersonal space. J. Neurosci. 32, 12921–12927. http://www.ncbi.nlm.nih.gov/pubmed/22973016 [Accessed December 22, 2014].
Sambo, C.F., Liang, M., Cruccu, G., Iannetti, G.D., 2012b. Defensive peripersonal space: the blink reflex evoked by hand stimulation is increased when the hand is near the face. J. Neurophysiol. 107, 880–889. Available at: http://jn.physiology.org/content/107/3/880 [Accessed December 15, 2015].
Scholkmann, F., Wolf, M., 2013. General equation for the differential pathlength factor of the frontal human head depending on wavelength and age. J. Biomed. Opt. 18, 105004.
Shen, G., Smyk, N.J., Meltzoff, A.N., Marshall, P.J., 2018. Neuropsychology of Human body parts: exploring categorical boundaries of tactile perception using somatosensory mismatch responses. J. Cogn. Neurosci. 30, 1858–1869.
Tsakiris, M., Costantini, M., Haggard, P., 2008. The role of the right temporo-parietal junction in maintaining a coherent sense of one's body. Neuropsychologia 46, 3014–3018.
van Belle, J., Vink, M., Durston, S., Zandbelt, B.B., 2014. Common and unique neural networks for proactive and reactive response inhibition revealed by independent component analysis of functional MRI data. Neuroimage 103, 65–74.
Versace, V., Campostrini, S., Sebastianelli, L., Saltuari, L., Solé, J.V., Kofler, M., 2021. Prepulse inhibition vs cognitive modulation of the hand blink reflex. Sci. Rep. 11, 1–10. https://doi.org/10.1038/s41598-021-84241-6.
Vieira, J.B., Pierzchajlo, S.R., Mitchell, D.G.V., 2020. Neural correlates of social and non-social personal space intrusions: role of defensive and peripersonal space systems in interpersonal distance regulation. Soc. Neurosci. 15, 36–51.
Viviani, R., 2013. Emotion regulation, attention to emotion, and the ventral attentional network. Front. Hum. Neurosci. 7, 1–24.
Zimeo Morais, G.A., Balardin, J.B., Sato, J.R., 2018. FNIRS Optodes' Location decider (fOLD): a toolbox for probe arrangement guided by brain regions-of-interest. Sci. Rep. 8, 1–11.