



Non-spatial skills differ in the front and rear peri-personal space

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ARTICLE INFO

Keywords:

Peri-personal space
oddball
Pupil
Multisensory calibration

ABSTRACT

In measuring behavioural and pupillary responses to auditory oddball stimuli delivered in the front and rear peri-personal space, we find that pupils dilate in response to rare stimuli, both target and distracters. Dilation in response to targets is stronger than the response to distracters, implying a task relevance effect on pupil responses. Crucially, pupil dilation in response to targets is also selectively modulated by the location of sound sources: stronger in the front than in the rear peri-personal space, in spite of matching behavioural performance. This supports the concept that even non-spatial skills, such as the ability to alert in response to behaviourally relevant events, are differentially engaged across subregions of the peri-personal space.

1. Introduction

There is growing evidence that space around the body is split into multiple subregions. These are encoded by partially distinct neural networks (di Pellegrino and Làdavas, 2015; Galati et al., 2000; Graziano and Gross, 1998) and served by different sensory modalities: for example, vision is obviously only available for the space in front of us, and haptics is primarily used in this region. This might generate asymmetries between spatial subregions, since prior work indicates that vision and haptics play an essential role in the development of specific perceptual and cognitive capabilities. While adult individuals integrate information across sensory modalities in a near-optimal way, children younger than 8–10 years combine multisensory signals in a qualitatively different way (Gori et al., 2008) – as complementary cues, where the most accurate sense calibrates or “trains” the others (Gori, 2015). Strong support for this concept came from the observation that lack of information from one sensory modality during these critical developmental stages, leads to inaccurate and imprecise processing in the other (intact) senses. For example, visual disabilities during childhood result in impaired spatial processing in non-visual tasks; similarly, motor disabilities, that prevent the deployment of haptics signals during early childhood, result in impaired visual size judgments (Cappagli et al., 2015; Finocchietti et al., 2015; Gori, 2015; Gori et al., 2016, 2014, 2010; Vercillo et al., 2016). Interestingly, a relative impairment of spatial processing may also be observed in healthy participants, performing

task in the rear space, by definition inaccessible to vision, and largely unexplored through haptics (Aggius-Vella et al., 2017a, 2018, 2020). These findings suggest that vision and haptics play a critical role in calibrating auditory spatial processing. Crucially, they support the notion that different subregions of space are endowed with different spatial skills, depending on the senses that serve them, and possibly due to “training” from different sensory modalities.

It is currently unknown, however, whether non-spatial abilities also differ across subregions of space. We hypothesized that auditory stimuli delivered to the front peri-personal space would have preferential processing compared to stimuli in the rear space, possibly due to the training from vision and haptics. We tested this hypothesis by probing an essential non-spatial skill, the ability to regulate alertness in response to behaviourally relevant events. We measured it with a classic task, auditory oddball. When a rare event occurs in a stream of repetitive events, it generates an “orienting” response. This consists of a characteristic scalp potential (p300 or p3), accompanied by autonomic correlates (e.g. the dilation of the eye pupil and increased perspiration), all preparing the organism to react to the change (Kamp and Donchin, 2015; Nieuwenhuis et al., 2011; Polich, 2007). The substrates of this complex reaction have been thoroughly investigated. They involve the two main attentional networks: the “saliency” or “ventral” attention network and the “orienting/monitoring” or “dorsal” networks (Brázdil et al., 2007; Corbetta et al., 1998; Corbetta and Shulman, 1998; Kim, 2014; Posner and Petersen, 1990). Oddball responses and their

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<https://doi.org/10.1016/j.neuropsychologia.2020.107619>

Received 18 March 2020; Received in revised form 25 July 2020; Accepted 2 September 2020

Available online 6 September 2020

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substrates have been generally found to be multimodal, in the sense that visual, auditory or other stimuli similarly recruit them. This suggests that different sensory modalities generally cooperate in refining activity in these networks, optimizing the efficiency of the behavioural response. Consequently, we hypothesize that the effectiveness of responses is reduced for subregions of space that are inaccessible to most sensory modalities, such as the rear space. The most marked differences in terms of response efficiency should be observed within the peri-personal space, defined as the region of space surrounding our bodies in which stimuli can be grasped, in contrast to extra-personal space that is extended beyond grasping distance and where exploratory eye movements occur (di Pellegrino and Làdavas, 2015). Peri-personal space is composed of a front subregion accessible to all three of our main sensory systems (vision, haptics and audition), and a rear subregion that is primarily accessible to audition. We therefore designed our study to compare oddball responses (behavioural and pupillary) to sounds presented in the front and rear peri-personal space of sighted adult individuals.

Most authors assume that the p300/p3 component of EEG scalp potentials and the pupil dilation response share a common origin, which may be placed in the activation of the Locus Coeruleus – Norepinephrine system, triggered by alerting events (Nieuwenhuis et al., 2011). Indeed, it is generally assumed that increased LC activity leads to pupil dilation – although the evidence supporting such a link has been sparse until recently, and it is still limited to particular cases (Costa and Rudebeck, 2016; Joshi et al., 2016; Murphy et al., 2011). A growing literature indicates that pupil size modulations, accompanying sensory events, are highly informative of their perceptual and cognitive processing (Beneditto and Binda, 2016; Binda et al., 2013; De Gee et al., 2014; Pomè et al., 2020; Turi et al., 2018) and often more informative than psychophysical measures. This suggests that pupil diameter represents a relatively accessible and rich source of information. Here we exploit it to reveal potential differences in response efficiency (operationalized as the strength of oddball effects) between the front and rear peri-personal space.

2. Method

2.1. Participants

Twenty-eight participants (12 females), with a mean age of 30 and standard deviation of 12 years, took part in this study. The sample size was estimated through power analysis, taking an estimate of effect size from previous work (Murphy et al., 2011) - with the desired power of .80. We estimated a minimum of 24 participants, and we recruited a few more to account for possible drop-outs or exclusions, which we did not have. At a later time point, we recruited a new sample of 15 participants (14 females) for a small replication study. All participants had a normal or corrected-to-normal vision and no history of psychiatric illness or head injury. They provided written informed consent in accordance with the Declaration of Helsinki. The study was approved by the ethics committee of the local health service (Comitato Etico, ASL3 Genovese, Italy).

2.2. Auditory oddball task

We used the three-stimulus variant of the oddball task (Comerchero and Polich, 1999). Stimuli were generated in Matlab (R2015b, The MathWorks) and delivered through the Psychophysical toolbox (Brainard, 1997; Pelli, 1997). They were 60-ms long sinusoidal tones with frequencies: 1940 Hz (standards), 2000 Hz (targets), and 500 Hz (distracters). Targets and distracters were pseudo-randomly interspersed amongst standards and each constituted 10% of the total number of trials. Tones were presented at an interstimulus interval (ISI) that varied pseudorandomly between 2.1 and 2.9 s. The stimuli were ordered such that at least three standard tones were presented between targets,

leaving a minimum inter-target interval of 8 s. This allowed sufficient time for the target-evoked pupil dilation to return to baseline.

In the main experiment, stimuli were presented through two speakers, which were placed in the front or rear peri-personal space at 50 cm from the participant (see Fig. 1). Participants performed two sessions, which differed only for the location of sound source: one had sounds coming from the front speakers, one from the rear speakers. The order of sessions was counterbalanced across participants. Upon post-experiment debriefing, 24 out of 28 participants reported that they did not notice that the sounds came from different directions across sessions, consistent with front back errors (Wightman and Kistler, 1999) related to the concept of cone of confusion in auditory localization (Carlile et al., 2005), and in line with previous experiments in our laboratory (Agius-Vella et al., 2019, 2017b; 2017a). Note that participants were not asked to localize sounds until the end of the experiment, and they were never given any feedback; the results of this informal questioning are equally consistent with participants making mislocalization errors (incorrectly attributing sounds from the rear to the front space or viceversa) or simply participants being unaware of the sound source location (given that this was not relevant to the task they performed during the experiment).

Participants were instructed to respond to target tones with a right index finger mouse click as accurately as possible (instructions did not emphasize the need for speeded responses) while ignoring the presentation of the nontarget and standard tones. They completed a practice run of the task to ensure that they were well acquainted with the instructions and with the three types of sounds. Participants were seated comfortably at a distance of 50 cm from a monitor screen, with their head supported by a chin rest, and were instructed to maintain their gaze

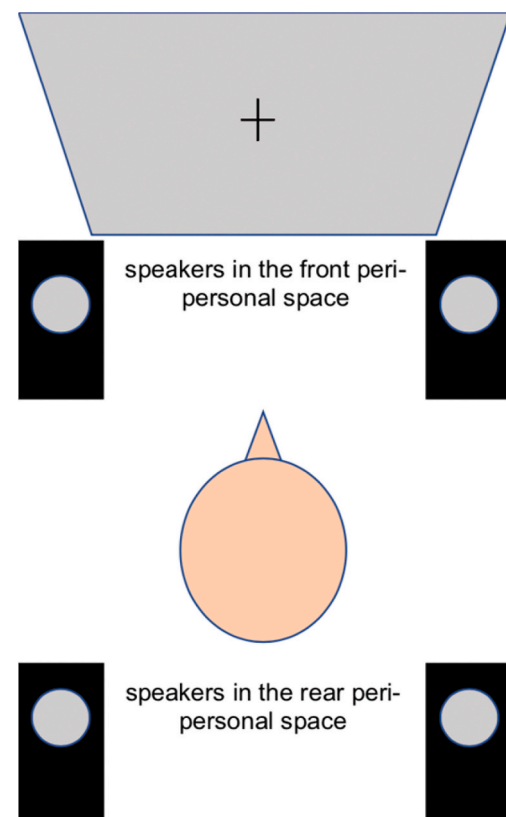


Fig. 1. Schematics of the experimental set-up. Participants sat 50 cm from the monitor and speakers. They were instructed to maintain gaze on a black fixation cross presented over a grey background at the centre of the monitor, while sounds were delivered through either the front speakers or the rear ones (in separate sessions). In the replication study, speakers were only present on the left side of the head.

on a central black fixation cross presented over a grey background.

There were 500 trials and 4 mandatory pauses of 1 min each. Between the two sessions, participants took a 10 min break. The total duration of the experiment, including instructions, practice trials, and the two sessions, was 40–50 min.

2.3. Eye tracking procedure and data preprocessing

Pupil diameter was measured monocularly with a fixation monitor (CRS LiveTrack system, Cambridge Research Systems) at 30 Hz, using an infrared camera mounted below the screen. Pupil diameter measurements were transformed from pixels to millimetres after calibrating the tracker with an artificial 4 mm pupil, positioned at the approximate location of each participants' left eye.

An off-line analysis examined the eye-tracking output to exclude time-points with unrealistic pupil-size recordings (where the pupil diameter was <0.1 mm, where the absolute value of its derivative was >0.1 mm, or where the absolute change over the trial was >1 mm). The remaining time-points were then interpolated at 20 Hz over a 2s interval (over which all trials could be defined). For each trial, we estimated a pupil baseline value in the first 100 ms and subtracted this from the pupil trace before estimating the pupil response, which we computed by averaging pupil diameter over the entire trace except the 100 ms used as a baseline. We used this approach to avoid making a priori assumptions on the exact temporal window over which pupil responses would develop; however, this is likely to attenuate differences across conditions. Therefore, we additionally report results from an alternative analysis approach where we measured the peak pupil dilation over the entire trace after the 100 ms used as baseline.

The average percentage of valid trials (for which a pupil response could be computed) was $66 \pm 4\%$ and $68 \pm 3\%$ for sounds in the front and rear space respectively – indistinguishable: ($t_{(27)} = 0.42$, $p = 0.6773$, $\log\text{-BF} = -0.66$).

2.4. Replication study

After the conclusion of this experiment, we performed a small replication study on 15 new participants (12 females). The paradigm and general arrangement were the same, with the exception that sounds were delivered by one of two speakers fitted in the front-left or rear-left corner of a sound insulated cabin (PUMA srl). Like in the main experiment, sounds in the front and rear space were tested in two separate sessions, with order counterbalanced across participants; upon debriefing, none of these reported sounds as coming from different locations in the two sessions. Pupillometry data were collected with a different system (Eyelink Duo, SR Research) fitted outside the cabin and measuring through its glass window in head-free mode (there was no chin rest and participants were simply asked to minimize head movements while keeping their gaze on the fixation target). This system has better temporal resolution (500 Hz) than the CRS used for the main experiment, but it did not allow for conversion from square pixels (measuring pupil area) to mm.

2.5. Statistical analyses

Statistical analyses took a standard repeated measure approach, which required averaging measures across trials to obtain six averages per participant: 2 sound location \times 3 sound types. We analysed the variance in behavioural and pupillometric measurements by using standard MATLAB functions provided with the Statistics and Machine Learning Toolbox (R2015b, The MathWorks). Specifically, we ran the function “fitrm (data, model)”, yielding an object “rm” with associated method “rANOVA” which returned F statistics with associated degrees of freedom, and P values for each of the main effects and their interaction.

The standard inferential approach (using p-values to define significance) was complemented with the estimation of Bayes factors. The JZS

Bayes Factor (Rouder et al., 2009) quantifies the evidence for or against the null hypothesis as the ratio of the likelihoods for the experimental and the null hypothesis. It can be expressed as the base-10 logarithm of the ratio (log-Bayes Factor or lgBF), where negative numbers indicate that the null hypothesis is likely to be true, positive that it is false. By convention, absolute lgBF greater than 0.5 are considered substantial evidence for or against the experimental hypothesis, and absolute log-factors greater than 1 strong evidence. For each post-hoc t-test, we also computed Cohen's d (Cohen, 1988) as a measure of effect size; by convention, a d of 0.5 is a medium effect size, 0.2 is a small effect size and 0.8 a large one.

We complement the standard repeated measures analysis with a second approach, particularly common in the field of pupillometry, namely the Linear Mixed model approach. In this approach, data from individual trials in all participants are modelled assuming the effects of experimental variables (“fixed effects”, namely sound location and sound type) and also accounting for the variability across participants (“random effects”, coded by allowing subject-by-subject variations of the intercept of the model). This analysis was implemented with the Matlab function “fitlme (data, model)”, yielding an object “lme” with associated method “ANOVA”, which returned F statistics with associated degrees of freedom, and P values for each of the fixed effects and their interaction.

Finally, correlation analyses (e.g. of behavioural and pupillary responses) were computed with the Matlab function “corrcoeff”, which outputs a correlation coefficient and its 95% confidence interval and associated p-value.

3. Results

We recorded pupil diameter variations while participants were engaged in a three-stimulus auditory odd-ball task. They pressed a key to detect the targets and withheld the keypress for distracters and standard sounds (Fig. 2A shows the distribution of reaction times for correct keypresses). In two consecutive sessions with randomized order, sounds came from (unseen) speakers placed in the front or the rear peri-personal space of the participant.

As shown in Fig. 2B, we found that rare sounds (both target and distracters) elicited a robust pupil dilation response, which was barely detectable for frequent sounds. The very small amplitude of responses to frequent sounds is not likely due to the statistical structure of our task, given that it was consistent across trials and did not show temporal evolution (the average response in the first 50 trials of the first session and in the last 50 trials of the last session were indistinguishable: ($t_{(25)} = -0.30$, $p = 0.7668$, $\log\text{-BF} = -0.67$). Importantly, the pupil response to the target sounds was larger than the response to distracter sounds, and it was selectively modulated by the location of sound sources: larger in the front space. We quantified this effect by computing the average baseline-corrected pupil dilation over the full-trial duration (Fig. 3A) and submitted it to a two-way ANOVA for repeated measures with factors sound-type (standard, distracter, and target) and space (front and rear). This revealed a significant interaction between the two factors ($F_{(2,27)} = 3.78176$, $p = 0.029$), a main effect for spatial position ($F_{(1,27)} = 4.72284$, $p = 0.039$) and a main effect of condition ($F_{(2,27)} = 69.63602$, $p < 0.001$).

We explored this with post-hoc paired t-tests and the scatterplots in Fig. 4A–C. The primary aim of this figure is to visualize the distribution of results from individual participants for sounds in the front (x-axis) and rear space (y-axis), relative to the bisection of the axes ($y = x$ line, dashed in the Figure). Where the majority of data points lays below the bisection line, the response to sounds in the front space is higher than in the rear space (as in Fig. 4A). This indicates that pupillary responses to target sounds in the front are significantly stronger than in the rear ($t_{(27)} = 3.30$, $p = 0.002$, $\lg\text{BF} = 1.14$, Cohen's d = 0.51, Fig. 4A) – a medium effect size according to Cohen's classification (Cohen, 1988). However, responses are strictly comparable for distracters ($t_{(27)} = 0.39$, $p = 0.696$,

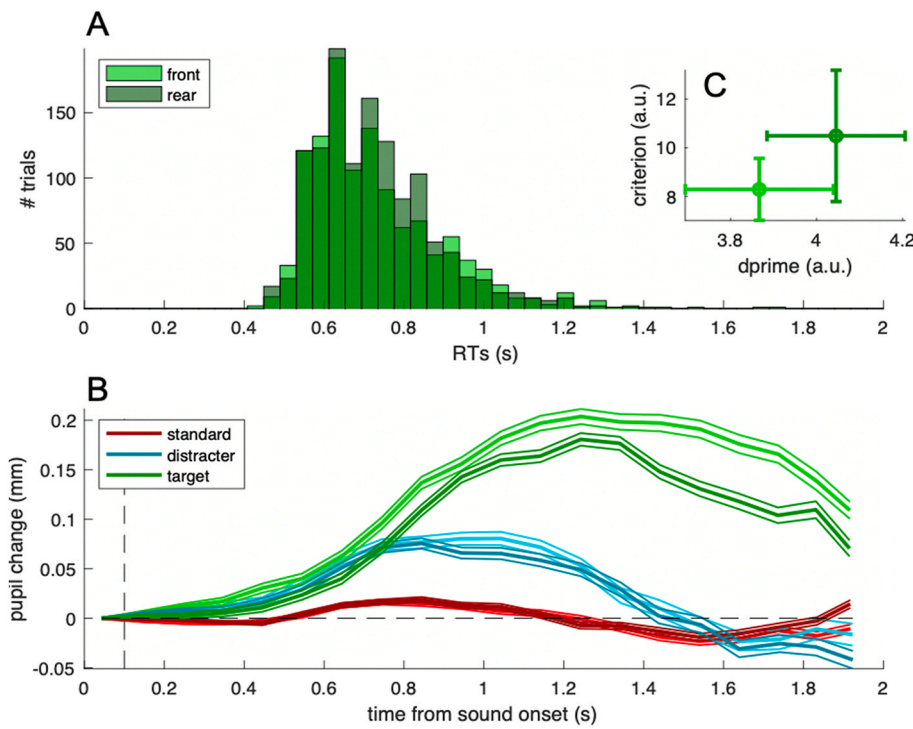


Fig. 2. Behavioural and pupillary oddball responses. A: distribution of reaction times for correctly detected target-sounds, computed after pooling trials across participants, separately for sounds delivered in the front (light green) or rear (dark green) peri-personal space. B: time-courses of pupil dilation, computed after pooling traces across participants and subtracting the pupil baseline (first 100 ms, marked by the dashed vertical line) from each trace. Time-courses are shown for each stimulus type (see legend) and space (darker colours for rear space). Thick lines give the average and thin lines the s.e.m. across trials. C: dprime and criterion values in the front and rear space, computed for each participant and then averaged; errorbars give the s.e.m. across participants.

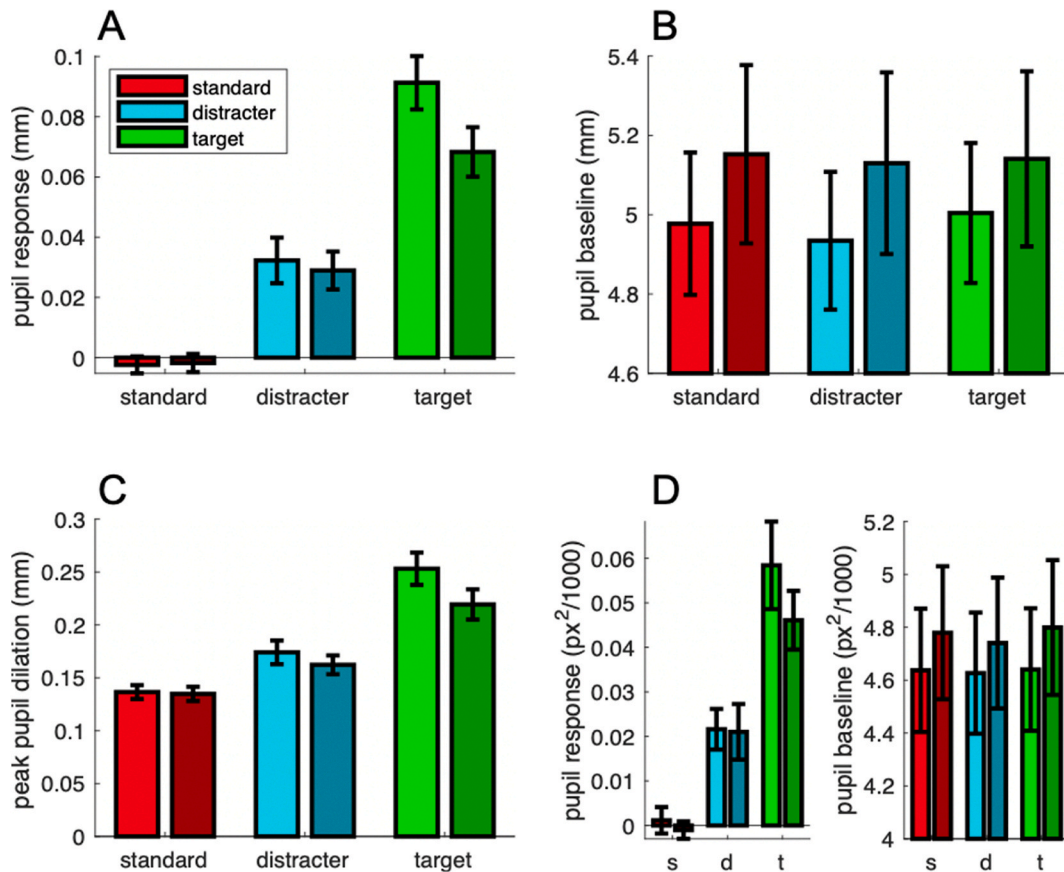


Fig. 3. Summary of pupillary behavior across sound locations and types. (A–C) show results from the main experiment. Average pupil response (A) pupil baseline (B) and peak dilation response relative to baseline (C) computed for target, distracter and standard sounds (see legend) presented in the front (lighter colours) and rear space (darker colours); error bars are s.e.m. across participants. (D) shows the results from the replication study, reporting the average pupil response and the baseline pupil size (both defined as pupil area in pixel).

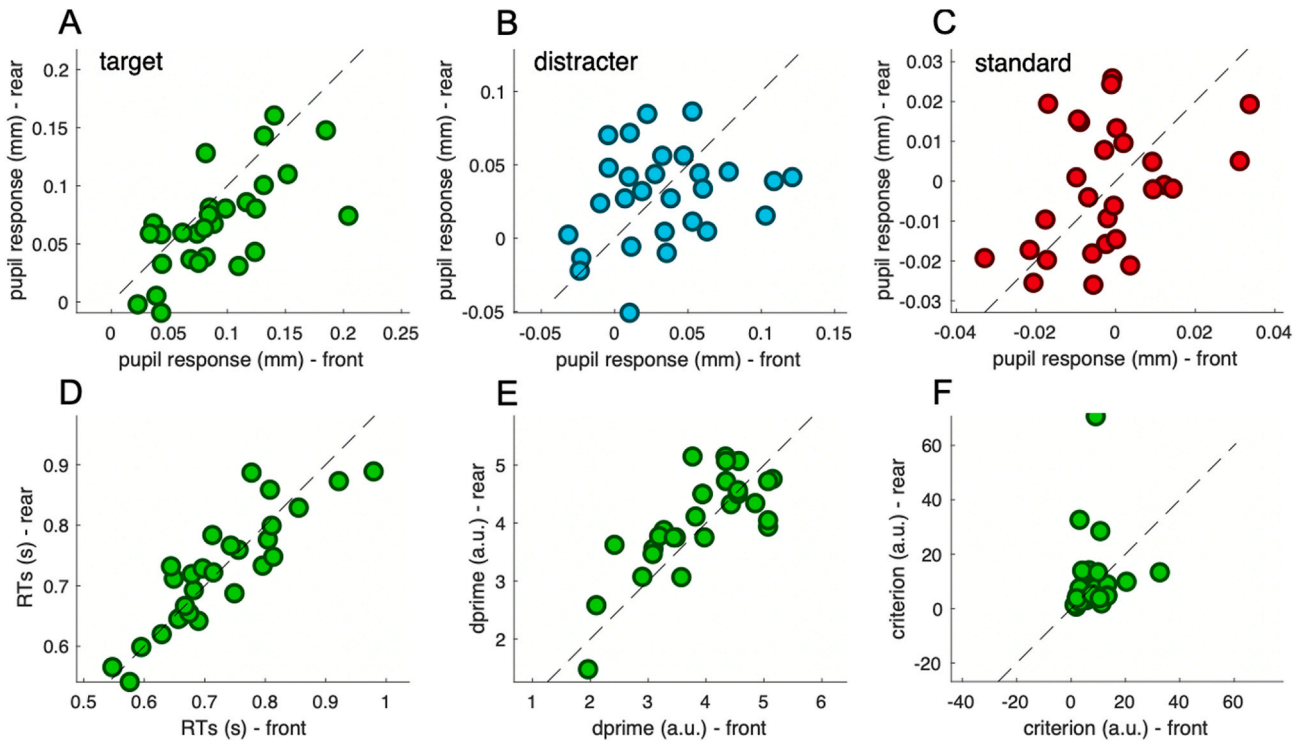


Fig. 4. Individual participants' results in the rear vs. front sessions. Each plot shows indices of responses to rear sounds, against corresponding indices for front sounds; the dashed line shows the $y = x$ function, implying equality between the two spaces. Top row: pupil responses to the three stimulus types (A: targets, B: distracters and C: standards). Bottom row: indices of behavioural performance (D: reaction times for correct target detections, E: d-prime and F: criterion).

lgBF = -0.67 , Cohen's $d = 0.08$, Fig. 4B) and standards ($t_{(27)} = -0.20$, $p = 0.846$, lgBF = -0.69 , Cohen's $d = 0.25$, Fig. 4C) – in both cases, data points are scattered around the bisection of the axes.

Fig. 3B also shows pupil-baseline measurements across stimulus types and spaces, for which we found a non-significant trend for larger pupil diameter in the rear space ($F_{(1,27)} = 1.51163$, $p = 0.229$), with no significant stimulus \times space interaction ($F_{(2,27)} = 1.29450$, $p = 0.282$) or main effect of stimulus type ($F_{(2,27)} = 2.31512$, $p = 0.108$).

We corroborated the results of our main analysis with two checks. First, we used an alternative index of pupil dilation: rather than averaging pupil size over the entire trial except the baseline window (which is likely to attenuate responses and thereby differences across conditions), we computed the peak pupil dilation in the same interval (Fig. 3C). Analyses of this index confirmed a highly significant stimulus type \times space interaction ($F_{(2,27)} = 4.92948$, $p = 0.011$); the main effect of spatial position ($F_{(1,27)} = 4.32758$, $p = 0.047$) and stimulus type ($F_{(2,27)} = 75.06840$, $p < 0.001$) were both significant. Second, we confirmed our inferences with an alternative statistical approach: the Linear Mixed Model. By analysing peak pupil dilations from individual trials with a linear model of the interaction between fixed effects (stimulus type and space) plus a random intercept to account for variability across participants, we confirmed a highly significant interaction between the two fixed factors ($F_{(2,19000)} = 7.04869$, $p < 0.001$), with a significant main effect of stimulus type ($F_{(2,19000)} = 232.07603$, $p < 0.001$) and no main effect of stimulus position ($F_{(2,19000)} = 0.28696$, $p = 0.592$).

Moreover, Fig. 3D shows the results from a replication study performed with slightly different equipment. In spite of the small number of participants ($N = 15$), the results recapitulate the main findings from the main experiment, showing enhancement of pupil responses to target sounds in the front vs. rear space ($t_{(14)} = 2.19$, $p = 0.046$, lgBF = 0.22 , Cohen's $d = 0.39$) but no difference between spaces for the distracter ($t_{(14)} = 0.09$, $p = 0.932$, lgBF = -0.58 , Cohen's $d = 0.03$) and standard sounds ($t_{(14)} = 0.65$, $p = 0.525$, lgBF = -0.50 , Cohen's $d = 0.01$). In

addition, like for the main experiment, we see a numerical trend (non significant) for larger baseline pupil size in the sessions where sounds came from the rear space ($t_{(14)} = -1.83$, $p = 0.089$, lgBF = -0.00 , Cohen's $d = 0.16$).

Fig. 4D–F shows how behavioural performance did not reliably differ across spaces – contrary to pupil responses, but coherently with the participants' self reports that sounds in the two spaces were generally indistinguishable (see methods). Reaction times were well matched for front and rear target sounds ($F_{(1,27)} = 0.0003$, $p = 0.986$), as shown by the overlapping distributions in Fig. 2A and the scatterplots in Fig. 4D. Similarly, the percentage of correct responses was not significantly modulated by sound location; the percentage of hits was 91.0% and 92.1% for targets. The percentage of false alarms was 1.1% and 0.7% for standards and 0.8% and 1.0% for distracters in the front and rear spaces, respectively. We used Signal Detection Theory to combine these values into estimates of sensitivity (d-prime) and bias (criterion) – using the log-linear approach to correct for ceiling or flooring effects (Hautus, 1995). These were very similar across spaces (see Fig. 2C and scatterplots in Fig. 4E–F, where data points scatter around the bisection of the axes marked by the dashed line), implying that different behavioural performance cannot explain away the differences in pupillometric indices. Indeed, if anything, there was a small non-significant trend for lower sensitivity in the front space compared to the rear one. This is logically opposite to the modulation of the pupil response that differentiated targets from non-target sounds better in the front space compared to the rear one.

Thus, as Figs. 2–4 show, the sound location appears to have a differential impact on pupillometry and behavioural measurements. We verified that this is not due to the general unreliability of behavioural parameters by averaging values across spaces and then testing across-subjects correlations between behavioural and pupillometric parameters. As shown in Fig. 5, we found that sensitivity is negatively correlated with reaction times (participants with better sensitivity had faster reaction times, Fig. 5A: $r = -0.49$, 95% confidence interval: $[-0.73 -0.14]$,

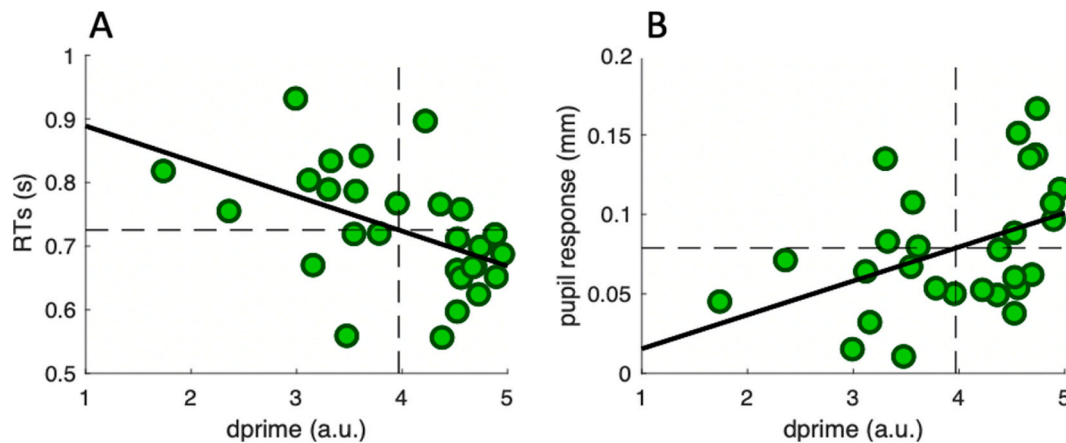


Fig. 5. Internal consistency of behavioural and pupillometry indices. Correlations across participants of dprime and average RT values (negatively correlated) and dprime and pupil response values (positively correlated), computed after pooling across sessions (i.e. averaged between front and rear sounds).

$p = 0.009$, $IgBF = 0.65$) and weakly correlated with the pupil dilation response to target sounds (participants with better sensitivity also tended to show larger pupil dilation responses, Fig. 5B: $r = 0.43$, C.I.: [0.07 0.69], $p = 0.021$, $IgBF = 0.31$). Criterion values, on the other hand, were not reliably associated with any variable (including d-prime values).

4. Discussion

We tested the hypothesis that non-spatial processing is enhanced in the regions of space that are usually accessible to multiple modalities. In particular, we asked whether the front peri-personal space (usually accessible to vision, haptics and audition) is superior to the rear peri-personal space (accessible only through audition). To address this question, we tested a basic form of non-spatial processing: the ability to alert to a stimulus. We measured this with a standard paradigm, the auditory oddball, and we compared pupil responses to oddball stimuli in the front and rear space.

We used a three-stimulus version of the paradigm (Comerchero and Polich, 1999). This task included two types of oddball stimuli: a target, which was only slightly different from the frequent sounds and prompted participants to execute a motor act (keypress), and a distracter, which was markedly deviant from the frequent sounds but was to be ignored. We found that both types of infrequent stimuli elicit a reliable pupil dilation response; however, the response is stronger for the target, in line with previous evidence that the oddball pupil response is modulated by task relevance (Kamp and Donchin, 2015). This evidence has been used to air the possibility that pupil dilation is a mere reflection of the motor activation required for the manual response – under this assumption, the relevance of pupil dilations for indexing stimulus processing would drop dramatically. However, our results speak directly against this possibility, by providing clear evidence that the pupil dilation response is modulated by a factor that leaves manual responses unaffected: the location of sound sources.

Specifically, we find that pupillary responses to target sounds in the front peri-personal space are larger than responses to sounds in the rear space. This difference is seen despite strictly matched manual reaction times between spaces (and in spite of good evidence that our indices of behavioural performance are internally coherent and well correlated with pupillary responses). Importantly, we also find that sound location selectively affects pupil responses to target sounds, whereas pupil dilation responses to distracter sounds are strictly matched between front and rear spaces. Together, these observations imply that pupil dilation is neither a reflection of the motor act, nor a read-out of bottom-up salience, but rather results from the interaction between salience and task relevance, which produces enhanced alertness to behaviourally relevant sounds in the front peri-personal space.

Such a model is coherent with the established view that the oddball task recruits at least two distinct neurocognitive networks: a bottom-up saliency network, associated with the ventral attention system, and a top-down monitoring system, partially overlapping with the dorsal attention system (Chong et al., 2008; Corbetta et al., 1998; Corbetta and Shulman, 1998; Debener et al., 2002; Kim, 2014; Posner, 1980). Although oddball responses (p300, phasic pupil dilation and skin conductance responses) are primarily associated with activations in the ventral saliency network, the dorsal network is critical for explaining task-relevance effects (e.g. larger oddball responses for task-relevant stimuli). In line with this concept, we propose that the magnitude of the pupil oddball response reflects the combination of bottom-up salience and behavioural goals. While bottom-up processing is identical in the front and rear space, given the lack of asymmetries in the auditory system, the ability to categorize target and non-target stimuli may be enhanced in the front peri-personal space, where categorization had a life-long training and validating through haptic and visual signals (absent from the rear space).

A similar concept has been introduced to explain differences in spatial abilities across front and rear spaces, suggesting that visual and haptic signals are critical for developing an accurate auditory spatial metric (Gori et al., 2010, 2014). This hypothesis also correctly predicts that blind individuals show subtle spatial deficits (Avraamides et al., 2004; Finocchiotti et al., 2015; Gori, 2015; Gori et al., 2014; Vercillo et al., 2016, 2018). The present results extend this hypothesis to non-spatial domains, suggesting that visual and/or haptic experience helps to develop the ability to categorize sounds even along non-spatial dimensions. Partly consistent with this hypothesis, there is evidence that oddball auditory tasks evoke distinct EEG responses in congenitally blind individuals. These recruit a more extensive network of areas than sighted individuals, and differences appear to primarily affect the late stages of auditory processing (Kujala et al., 1997, 1995a; 1995b).

These results provide clear evidence that peri-personal space is not a unitary construct (Berti and Frassinetti, 1996; di Pellegrino and Làdavas, 2015; Farnè et al., 2005; Farnè and Làdavas, 2002; Iachini et al., 2016; Làdavas and Serino, 2008; Noel et al., 2016, 2015a; Serino et al., 2015, 2011). It may be split into at least two sub-regions, accessible through different sensory modalities and consequently different cognitive skills. Importantly, we show that differences involve alertness, which is one of the features that delimit peri-personal from extra-personal space. Prior work has shown that the limit between peri- and extra-personal space is farther in the front than in the rear (Noel et al., 2015b). Our results indicate that the front peri-personal space is also endowed with superior alertness for behaviourally relevant events – while the two sub-regions of space are matched in terms of bottom-up salience. Note that post-experiment questioning revealed that participants were generally

unaware of the difference in sound source location across sessions, suggesting that conscious spatial processing and non-spatial processing (as engaged in the oddball paradigm) may be dissociated.

While the superiority of the front peri-personal space emerges clearly in the involuntary pupil response, it does not show in any of the parameters of the voluntary responses that we recorded. This might be due entirely to methodological issues. Our task was a go/no go paradigm, implying that RTs could only be measured for targets and preventing the possibility to compare them across stimulus categories; moreover, instructions emphasized accuracy over speed. An alternative and possibly more interesting explanation is related to the additional motivational and metacognitive components that are involved in generating voluntary responses, compared to the automatic pupillary responses. For example, if participants felt that the task was more difficult on a given session, they might have faced it with a different cognitive strategy, dedicating additional attentional resources. Such a strategy could guarantee identical behavioural performance across sessions with sounds in the front or rear peri-personal space. Alternatively, one could speculate that sounds approaching from behind is often associated with a hazard and therefore automatically calls for additional processing resources. Both these scenarios predict that sessions with sounds from the rear should be characterized by increased cognitive effort, and consequently a tonic increase of pre-stimulus pupil diameter (i.e. baseline pupil diameter), given the oft-assumed link between cognitive effort, tonic activation of the Locus Coeruleus – Norepinephrine system, and steady pupil dilation (Costa and Rudebeck, 2016; Joshi et al., 2016; Murphy et al., 2011). Our data do show a numerical trend for steadily larger pupil diameter in sessions with sounds from the rear peri-personal space (both in the original and in the replication study), although the effect does not reach statistical significance. In this respect, we note that pupil size changes observed over minutes (sessions) are difficult to detect due to the numerous factors that simultaneously affect the regulation of pupil diameter in disparate directions: from light adaptation to fatigue (Loewenfeld and Lowenstein, 1993). Relatedly, we note that previous research has placed much emphasis on oscillations of pre-stimulus pupil diameter predicting stimulus-evoked responses: pupillometric, behavioural or EEG (Kamp and Donchin, 2015; Murphy et al., 2011). We did not attempt to replicate these analyses due to the short duration of our sessions (less than half of that used in previous studies), a limitation imposed by the necessity to administer two sessions per participant, with sounds coming from the two directions.

To summarize, our results corroborate the evidence that pupil responses can be used as a marker of stimulus processing (Murphy et al., 2014, 2011). They also indicate that it may be more sensitive than behavioural measures, as suggested in a variety of different contexts (Benedetto and Binda, 2016; Binda et al., 2013; Pomè et al., 2020; Turi et al., 2018). Using pupil recordings, we were able to reveal an asymmetry between two subregions of the peri-personal space: the front presents superior alertness for behaviourally relevant stimuli than the rear one. Our results show, for the first time, that differences between these two subregions involve non-spatial domains, suggesting a fundamental role of vision and haptics (absent from the rear space) for the training of both spatial and non-spatial cognitive abilities.

CRediT authorship contribution statement

Elena Aggius-Vella: Conceptualization, Investigation, Writing - original draft. **Monica Gori:** Supervision, Writing - review & editing. **Silvia Animalì:** Methodology, Investigation. **Claudio Campus:** Software, Writing - review & editing. **Paola Binda:** Conceptualization, Methodology, Formal analysis, Writing - original draft.

Acknowledgments

This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and

innovation programme (grant agreement No 801715 - PUPILTRAITS) and by the Ministry of University and Research under the programme PRIN 2017 (grant MISMATCH). The authors would like to thank Dr. Danilo Menicucci for help implementing the three-stimulus oddball paradigm.

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