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Limits of cross-modal plasticity? Short-term visual deprivation does not enhance cardiac interoception, thermosensation, or tactile spatial acuity

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Abstract

In the present study, we investigated the effect of short-term visual deprivation on discriminative touch, cardiac interoception, and thermosensation by asking 64 healthy volunteers to perform four behavioral tasks. The experimental group contained 32 subjects who were blindfolded and kept in complete darkness for 110 minutes, while the control group consisted of 32 volunteers who were not blindfolded but were otherwise kept under identical experimental conditions. Both groups performed the required tasks three times: before and directly after deprivation (or control) and after an additional washout period of 40 minutes, in which all participants were exposed to normal light conditions. Our results showed that short-term visual deprivation had no effect on any of the senses tested. This finding suggests that short-term visual deprivation does not modulate basic bodily senses and extends this principle beyond tactile processing to the interoceptive modalities of cardiac and thermal sensations.

Keywords: cross-modal plasticity, blindfolding, interoception, thermosensation, touch

1. Introduction

Neuroplasticity is the brain's capacity to adapt and change in response to phenomena such as learning, developmental factors, and aging as well as injury or a loss of peripheral input (see Pascual-Leone, Amedi, Fregni & Merabet, 2005). Cross-modal plasticity, a type of neuroplasticity, occurs after sensory deprivation, which could be a result of disease, brain damage, or other factors and can lead to the strengthening of one or more sensory systems to compensate for the lack of another, reflecting an adaptive strategy (see Merabet & Pascual-Leone, 2009). Among other hypotheses (see Singh, Phillips, Merabet & Sinha, 2018), it has been proposed that the source of these cross-modal changes could be a process of "unmasking" and subsequent strengthening of weak cross-modal connections that are suppressed under normal conditions (see Pascual-Leone & Hamilton, 2001; Merabet et al., 2007; Merabet et al., 2008; Striem-Amit, Cohen, Dehaene & Amedi, 2012; Qin & Yu, 2013; Lazzouni & Lepore, 2014). Indeed, such pre-existing cortico-cortical connections between, for example, visual areas and other (preserved) modality areas, which are suppressed under normal circumstances, could facilitate information transfer to the visual cortex (Schroeder et al., 2003; Ptito & Kupers, 2005; Masuda, Dumoulin, Nakadomari & Wandell, 2008; Cappe, Rouiller & Barone, 2009; Masuda et al., 2010). Given the compelling results from both animal and human studies (Convento, Vallar, Galantini & Bolognini, 2013; Humanes-Valera, Aguilar & Foffani, 2013; Makin & Bensmaia, 2017), the "unmasking" hypothesis is thought to explain at least some of the general processes observed in the reorganization of the adult cortex (see Singh et al., 2018). Although the specific mechanism underlying the rerouting of non-visual information to the visual cortex has not been fully understood, sensory deprivation studies remain an attractive method of exploring one of the most fascinating properties of the human brain, namely, plasticity.

A well-studied example of massive cross-modal plasticity is the neural changes that follow blindness. Those changes reportedly lead to enhancements in the following senses: touch (e.g., Goldreich & Kanics, 2006; Chebat, Rainville, Kupers & Ptito, 2007; Bauer, Yazzolino, Hirsch, Cattaneo, Vecchi & Merabet, 2015), hearing (e.g., Voss et al., 2004; Gougoux, Zatorre, Lassonde, Voss & Lepore, 2005; Collignon, Voss, Lassonde & Lepore, 2008), and smell (e.g., Rosenbluth, Grossman & Kaitz, 2000; Cuevas, Plaza, Rombaux, De Volder & Renier, 2009; Beaulieu-Lefebvre, Schneider, Kupers & Ptito, 2011; Kupers et al., 2011). Interestingly, a considerable number of studies have suggested that brain plasticity can also be triggered in healthy individuals by short-term visual deprivation for periods as short as 90 minutes – an observation that can shed light on the mechanisms of neuroplasticity (e.g., Facchini & Aglioti, 2003; Weisser et al., 2005; Lewald, 2007; Lazzouni, Voss & Lepore, 2012; Landry, Shiller & Champoux, 2013; Fengler, Nava & Röder, 2015; Pagé, Sharp, Landry & Champoux, 2016; Schwenk, Van Rullen & Bremmer, 2020; but see also: Wong, Hackeman, Hurd & Goldreich, 2011; Crabtree & Norman, 2014; Cambieri et al., 2017). Furthermore, it has been shown that blindfolding in sighted individuals leads to increased excitability of the visual cortex (Boroojerdi et al., 2000; Fierro et al., 2005), which may become engaged in processing non-visual stimuli (Weisser et al., 2005; Merabet et al., 2007; 2008). Taken together, there is evidence that visual deprivation through blindfolding reversibly affects several perceptual abilities, which indicates that short-term deprivation, to some degree, can produce similar perceptual effects as blindness (Merabet et al., 2008).

Recently, sensory abilities related to the body were shown to be altered following visual impairment; for example, studies have suggested that blind people discriminate heat better than sighted individuals (Slimani, Ptito & Kupers, 2015) and present lower pain thresholds for both cold and heat (Slimani et al., 2013). In addition to being somatosensory submodalities, these processes of temperature perception and heat pain have been reclassified as interoception based on anatomical considerations and the fact that they provide information about the physiological condition of the body, which is a key function of interoception (Craig, 2003a; see also: Khalsa et al., 2018). Classic definitions of interoception were originally focused on visceral sensations only (see Sherrington, 1948), whereas more recent accounts frame interoceptive signals more broadly and include stimuli mediated by the skin and transmitted through lamina I of the spinal cord, e.g., sharp and burning pain, innocuous warmth and cold, itch, or affective touch (see Purves et al., 2019). Such signals help the organism maintain an optimal internal state via the activation of homeostatic mechanisms (see von Mohr & Fotopoulou, 2018). Therefore, interoception, in its broader definition used in this paper, refers to signals originating from the internal body and visceral organs, such as cardiac or gastric sensations, as well as to skin-mediated signals that facilitate homeostasis, such as pain, thermal sensations or affective touch because of their motivational relevance in physiological regulation (see Craig, 2003b; Hua, Strigo, Baxter, Johnson & Craig, 2005; Björnsdotter, Morrison & Olausson, 2010; Fealey, 2013; Ceunen, Vlaeyen & Van Diest, 2016; Gentsch, Crucianelli, Jenkinson & Fotopoulou, 2016; Crucianelli, Krahé, Jenkinson & Fotopoulou, 2018; Gilam, Gross, Wager, Keefe & Mackey, 2020; Wei & Van Someren, 2020).

In a study by Noel et al. (2018) on audiovisual deprivation and cardiac interoceptive accuracy, a very short (15 minutes) deprivation through blindfolding and testing in an anechoic room did not alter interoceptive accuracy on a group level (approximately half of the participants showed improved interoceptive accuracy while the other half showed worse accuracy). It has also been shown that short-term deprivation of exteroceptive senses, including vision, through Reduced Environmental Stimulation Therapy (REST), leads to heightened interoceptive awareness in patients with high levels of anxiety sensitivity (Feinstein et al., 2018). Similarly, REST seems to decrease pain intensity ratings and pain widespreadness in patients with chronic pain (Loose, Manuel, Karst, Schmidt & Beissner, 2021). Interestingly, Zubek and colleagues (1964) showed that sighted subjects who were visually deprived for a week showed an increase in sensitivity to heat and pain. However, except for these studies, the influence of short-term purely visual deprivation has not yet been examined using a battery of interoceptive tasks, instead focusing on one interoceptive modality. Based on a number of behavioral studies of interoception in blind individuals showing hypersensitivity to heat and cold pain (Slimani et al., 2013), enhanced innocuous heat discrimination (Slimani et al., 2015) and faster central processing of C-fiber input (Slimani, Plaghki, Ptito & Kupers, 2016) following congenital blindness, it could be hypothesized that short-term visual deprivation can also have an effect on interoceptive modalities in sighted individuals.

One of the measures most often employed in interoception research is the heartbeat counting task (Dale & Anderson, 1978; Schandry, 1981), in which participants count their heartbeats for a given amount of time without touching their body and then their estimation is compared with the number of their real recorded heartbeats. The measurement is supposed to determine the participant's access to sensory information from the heart. The task is short and easy to implement, and it should offer a relatively direct measure of cardiac interoception. Compared with the classic cardioceptive heartbeat discrimination task (Katkin, Reed & Deroo, 1983), where participants need to judge whether a sequence of stimuli is presented in synchrony with their heartbeat or not, the heartbeat counting task also offers the advantage of not having additional potentially cofounding factors and task demands related to tones or flashes (see Garfinkel et al., 2016a). However, the heartbeat counting task has been criticized in recent years because the results may be influenced by several factors, such as beliefs about or knowledge of the resting heart rate as well as the heart rate itself (Ring, Brener, Knapp, & Mailloux, 2015; Murphy et al., 2018; Ring & Brener, 2018; Zamariola, Maurage, Luminet & Corneille, 2018).

Therefore, to identify additional measures of interoceptive submodalities, our group has recently developed a task focused on thermosensation, namely, the thermal matching task (Crucianelli, Enmalm & Ehrsson, 2021), in which participants are asked to identify a previously perceived thermal stimulus (i.e., a stroke on the skin) in a sequence of colder or warmer stimuli presented in increasing or decreasing order. The results obtained in two separate samples suggest that it is possible to broaden the testable interoceptive modalities beyond cardiac signals to include temperature perception and other skin-based modalities that supposedly also rely on input from C-fibers (Crucianelli et al., 2018, 2021).

In this experiment, we aimed to explore the role of short-term visual deprivation on tactile, thermosensory, and cardiac perception by asking 64 healthy sex-balanced volunteers to perform four behavioral tasks. Three different tasks focusing on two separate interoceptive submodalities, cardiac and thermosensory, were chosen to provide a multifaceted overview of the effects of short-term deprivation on interoception. Cardiac interoceptive perception was operationalized here as the degree of accuracy in the heartbeat counting task (Dale & Anderson, 1978; Schandry, 1981), while thermosensory perception was operationalized as the degree of accuracy in the newly established thermal matching task (Crucianelli et al., 2021) as well as the sensitivity and consistency in detecting temperature changes in the temperature detection task, a widely used task in clinical settings (Fruhstorfer, Lindblom & Schmidt, 1976; see also Heldestad, Linder, Sellersjö & Nordh, 2010). As a measure of tactile acuity, we implemented a commonly used test of passive tactile spatial acuity, the tactile grating orientation task (see Van Boven, Hamilton, Kauffman, Keenan & Pascual-Leone, 2000; Facchini & Aglioti, 2003; Wong et al., 2011a). Thirty-two test subjects were blindfolded and kept in complete darkness for 110 minutes, while the 32 control-group volunteers were not blindfolded and kept under the same experimental settings. Both groups performed the tasks three times: before and directly after deprivation (or control) and after an additional washout period of 40 minutes, in which all participants were exposed to normal light conditions. We tested the hypothesis that a short period of blindfolding would lead to reversible improvement of cardiac and thermal sensations. We thus predicted that in the thermal matching task, temperature detection task, and heartbeat counting task, participants in the deprived group would show significant improvement after blindfolding and that the effect would disappear when the blindfold was removed. We also re-examined the hypothesis (Facchini & Aglioti, 2003) that blindfolding would improve tactile acuity and predicted that in the tactile grating orientation task, the blindfolded group should show significantly better performance (higher acuity) than the control group.

2. Methods

2.1 Participants

The experiment was completed by a total of 64 healthy right-handed volunteers: 32 in the deprived group (mean age = 26.4, range = 18-39, 16 females, 16 males) and 32 in the non-deprived group (mean age = 26.5, range = 19-46, 16 females, 16 males). The sample size was determined before the experiment started and mirrored the previous study by Crucianelli et al. (2021), who included the same thermal matching and thermal detection tasks as used in the present study as well as the heartbeat counting task; moreover, this sample size is similar to those used before for blindfolding experiments on the tactile acuity task (e.g., Wong et al., 2011). Both groups were sex-balanced due to reports suggesting that women presented higher interoceptive sensibility (tendency to notice bodily sensations more often) but lower accuracy (Grabauskaitė, Baranauskas & Griškova-Bulanova, 2017) as well as a higher performance in the grating orientation task (Wong et al., 2011a). There was no significant difference in age between the groups (t(62) = –.077, p = .939). Body mass index (BMI) data were collected for the subjects since this parameter has been shown to influence cardiac interoceptive accuracy (Murphy, Geary, Millgate, Catmur & Bird, 2017). The BMI was 22.5 (SD = 3.3) for participants in the deprived group and 23.2 (SD = 5) in the non-deprived group, with no significant difference between groups (t(62) = –.68, p = .499). The average age and BMI were similar to values from other studies of interoception in healthy samples (e.g., Pollatos, Gramann & Schandry, 2006; Garfinkel, Seth, Barrett, Suzuki & Critchley, 2015).

Each subject was assigned to one of the two groups (deprived or non-deprived) according to a randomization schedule. The participants were recruited through advertisements on the campus of Karolinska Institutet and social media and tested within an 8-month period between July and February. All participants reported that they had normal or corrected-to-normal vision. Exclusion criteria included a history of neurological or psychiatric disorders, skin conditions (e.g., psoriasis) or alterations (scars, tattoos), and finger pad calluses or injuries because these conditions can affect the perception of touch, warmth and cold.

The study was approved by the Ethics Review Authority in Sweden (2016/2398-31/4 and 2019-03823), and the experiment was carried out in accordance with the approved guidelines. All participants provided written informed consent before the study. The participants were compensated for participation with 1000 SEK (an equivalent of €100). The source data used to generate all the Figures are provided in Appendix B.

2.2 Tasks and procedures

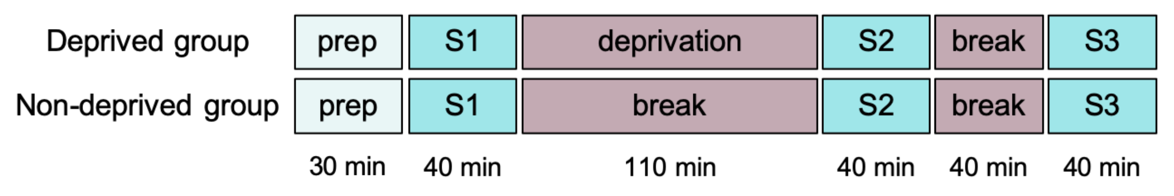

Figure 1. Timeline of the experiment. *Prep* represents the time allotted for the questionnaires and instructions. *S1*, *S2* and *S3* represent session I, session II and session III, respectively.

The three testing sessions (I, II, III) consisted of four tasks (see below) and were separated by fixed intervals (Figure 1). The order of tasks was kept constant across the sessions and groups: (1) heartbeat counting task, (2) thermal matching task, (3) tactile grating orientation task, and (4) temperature detection task (see Table 1). We decided on such order to avoid potential effect of thermal and tactile tasks demands on cardiac reactivity, and to separate two thermal tasks with a procedure focusing on another sensory modality. Both groups performed the tasks before and directly after deprivation (or control) and after an additional washout period of 40 minutes, in which all participants were exposed to normal room light conditions and could see the entirety of the testing room. The duration of blindfolding and washout was based on previous studies on short-term visual deprivation (e.g., Fierro et al., 2005; Weisser, Stilla, Peltier, Hu & Sathian, 2005; Lewald, 2007; Merabet et al., 2008; Landry et al., 2013). All of the subjects were blindfolded while performing the tasks to make the experimental conditions identical for both of the groups. The blindfold, which also covered the nose area, prevented all light from reaching the eyes; in the deprived group, medical tape was placed around the mask to avoid accidental displacement. Blinking or eye movements were not prevented by the blindfold. Only the subjects from the deprived group were blindfolded during the interval between sessions I and II, with the blindfold remaining in place from the end of session I to the end of session II, while the subjects from the control group removed the mask and were re-exposed to light after every task during session II. This design allows for a straightforward comparison of baseline performance (no procedural differences between the groups in session I) without potentially cofounding factors (i.e., possible effect of light deprivation already within session I due to the relatively long duration of the session). Participants were alert and listening to a previously prepared playlist of music or a podcast of their choice for the whole duration of the blindfolding/control. They were accompanied by the experimenter, who informed participants about the time left every 15 minutes and made sure that the participants did not show any signs of drowsiness or discomfort. All participants remained alert for the whole duration of the experiment and verbally reported to the experimenter by confirming they understood the information. In the deprived group, during session II, the lights in the room were turned off to ensure that the participants were indeed kept in complete darkness, and the experimenter conducted the task with the minimal light needed to apply the stimuli and record the answers. However, to further make sure that the blindfold indeed covered all the visual input, at the beginning of the deprivation period, participants were asked about their light perception under normal room illumination. Each volunteer confirmed that no light was noticed. Also, by the end of the experiment all participants confirmed that no light was noticed during the entire procedure involving the blindfold. Participants in the non-deprived group spent the remainder of the period in a room with normal light conditions. The same conditions of no view restrictions and normal light were administered for the period between sessions II and III (washout) for both groups. Upon experiment completion, all participants were debriefed about the purpose of the study.

Task order	**Task**	**Task description**	**Outcome measures**
1	Heartbeat counting task	6 trials (25 s, 30 s, 35 s, 40 s, 45 s, 50 s)	Values from 0–1
2	Thermal matching task	3 temperatures (30 °C, 32 °C, 34 °C) 2 body locations (palm and forearm) 2 orders of stimulation (warming and cooling)	Values from 0–1
3	Tactile grating orientation task	20 trials of up to 8 gratings	Grating of 70% accuracy

4	Temperature detection task	Method of limits 5 trials for warming, 5 trials for cooling	Temperature detection and standard deviations

Table 1. Overview of the structure of tasks. The basic tasks described in the order they were completed during the experimental procedure.

Participants were asked to fill out two questionnaires regarding their bodily experiences and psychological functioning (see *Questionnaires*) at the very beginning of the experiment prior to the behavioral tasks, which allowed for any potentially elevated heart rates due to walking/cycling fast pace to the building, etc. to return to a normal level in all participants since increased physiological arousal has been shown to provide an advantage for heartbeat perception (Pollatos, Herbert, Kaufmann, Auer & Schandry, 2007). For the same reason, participants were also asked not to consume any caffeinated drinks on the day of the experiment (see Hartley, Lovallo & Whitsett, 2004; McMullen, Whitehouse, Shine, Whitton, & Towell, 2012). Before the start of the first session, all participants were informed about the experimental setup and received a short description of the experiment. Then, the participants sat on a chair in a comfortable position. The temperature of the testing room was inspected before, during and after the experiment, and it was kept at approximately a neutral temperature of 22.5 °C. The subjects were well adjusted to the room temperature before starting the first behavioral task. All thermal tasks were conducted on the left nondominant palm or forearm, which is consistent with the procedures used in Crucianelli et al. (2021). The grating orientation task, however, was conducted on the right dominant index finger, in accordance with previous experiments on tactile acuity (Facchini & Aglioti, 2003; Wong et al., 2011a). All tasks were administered by the same experimenter (D.R.) in all participants.

2.2.1 Questionnaires

Participants were asked to complete two self-report questionnaires. The Body Awareness Questionnaire (BAQ; Shields, Mallory & Simon, 1989) is an 18-item scale measuring attentiveness to normal bodily processes. The Depression, Anxiety and Stress Scale (DASS-21; Lovibond & Lovibond, 1995) is a self-report questionnaire consisting of 21 items, with 7 items per subscale on depression, anxiety and stress. It was implemented to serve as a control measure for possible subclinical manifestations of depression, anxiety and stress, which have all been suggested to be associated with altered interoception (e.g., Dunn, Dalgleish, Ogilvie & Lawrence, 2007, Domschke, Stevens, Pfleiderer & Gerlach, 2010; Paulus & Stein, 2010, respectively). No significant differences emerged between the groups in any of the measurements (see Table 2).

	BAQ	**Depression**	**Anxiety**	**Stress**
Total sample	84.39 (12.84)	2.28 (2.52)	3.08 (3.19)	4.45 (3.33)
Deprived group	83.81 (11.34)	1.69 (1.96)	2.75 (2.90)	3.84 (2.92)
Non-deprived group	84.97 (14.35)	2.88 (2.88)	3.41 (3.48)	5.06 (3.64)
t (p) values	–.358 (.722)	–1.928 (.058)	–.820 (.415)	–1.478 (.144)

Table 2. Mean and standard deviations for the Body Awareness Questionnaire (BAQ) and each subscale of the Depression, Anxiety and Stress Scale (DASS-21).

2.2.2 Heartbeat counting task

A heart rate baseline reading was obtained over a 5-minute period before the beginning of the heartbeat counting task. The participants' heart rate was recorded using a Biopac MP150 BN-PPGED (Goleta, CA, United States) pulse oximeter attached to their nondominant (left) index finger and connected to a laptop with AcqKnowledge software (version 5.0), which recorded the number of heartbeats after preset time. The number of heartbeats was then quantified using the embedded 'count peaks' function. To reduce the possibility that participants would perceive the pulsation in fingers due to the grip of the pulse oximeter, which has been shown to facilitate the performance and inflate the confidence ratings (Murphy et al., 2019), special attention was focused on ensuring a comfortable and not overtight fit of the finger cuff. The resting heart rates were 74.38 BPM (SD = 7.38) in the deprived group and 75.85 BPM (SD = 12.37) in the non-deprived group in S1; 66.75 BPM (SD = 10.03) in the deprived group and 66.13 BPM (SD = 9.69) in the non-deprived group in S2; and 66.06 (SD = 10.80) in the deprived group and 66.17 (SD = 9.68) in the non-deprived group in S3. This finding is consistent with other experiments showing resting heart rates of 68-76 beats per minute for healthy people aged 20-39 years (Hart, 2015), which corresponded to the vast majority of our sample.

Participants were asked to breathe normally and given the following instructions: *Without manual checking, can you silently count each heartbeat you feel in your body from the time you hear "start" to when you hear "stop". Do not take your pulse. You are only allowed to feel the sensation of your heart beating*. A cue from the experimenter signaled when to start and stop counting. After the trial, the participants verbally reported the number of heartbeats counted, and they did not receive any feedback regarding their performance. Immediately after reporting the number of counted heartbeats, the participants were asked to rate their confidence in perceived accuracy of response (see Garfinkel et al., 2015). This confidence judgment was reported on a scale from 0 (total guess/no heartbeat awareness) to 10 (complete confidence/full perception of heartbeat). To produce a global measure of mean confidence in perceived accuracy of response, the mean confidence during the heartbeat counting task was calculated by averaging the confidence judgments over all experimental trials. The task was repeated six times to form six trials, using intervals of 25, 30, 35, 40, 45 and 50 seconds (as in the original procedure of Schandry, 1981), with a break of 30 seconds between intervals. Participants received no information about the interval length. The interval order was randomized between participants and sessions.

For each trial, an accuracy score was derived using the formula based on Schandry (1981):

$$\frac{1}{6}\Sigma(1-\frac{|recorded\ heartbeats - counted\ heartbeats|}{recorded\ heartbeats})$$

The resulting scores were averaged over 6 trials. The interoceptive accuracy scores obtained following this transformation usually vary between 0 and 1, with higher scores indicating a better discrimination of the heartbeats (i.e., smaller differences between estimated and actual heartbeats).

2.2.3 Thermosensory tasks

Before each thermal task, the temperature of the dorsal surface of the left hand and ventral surface of the left hand was measured using an infrared thermometer (Microlife NC 150, Taipei, Taiwan) at three different locations at each site to control for any significant individual differences in skin temperature that could potentially influence the performance in the task (for skin temperature values, see Supplementary Table 1). The thermal stimuli were delivered through a 25 x 50 mm thermode attached to a thermal stimulator (Somedic SenseLab AB, Hörby, Sweden), with a precision of ± 0.1-0.2 °C.

2.2.3.1 Thermal matching task

A range of non-noxious temperatures from 22 °C (cool) to neutral (32 °C; typical human arm skin temperature; Arens and Zhang, 2006) to 42 °C (warm) was applied. The temperatures were presented in a systematically increasing (from cool to warm) or decreasing (from warm to cool) order in trials consisting of gradual changes in temperature (2 °C at a time), with up to 9 increments in total. The participant's task was to verbally indicate the temperature that was presented at the beginning of the trial ("reference temperature"). The task was repeated six times to form six trials in an increasing/decreasing manner presented in a randomized order, with 30 °C, 32 °C and 34 °C (within the range of neutral/innocuous temperatures) used as reference temperatures. The temperature at the start of the trial was ± 8°C of the reference temperature (range from 22-38 °C for 30 °C; range from 24-40 °C for 32 °C; and range from 26-42 °C for 34 °C). The same procedure was introduced for the forearm (hairy skin) and palm (non-hairy skin). The starting the task from palm/forearm was counterbalanced across participants and sessions. The duration of each stroke was kept constant at 3 seconds, and the velocity of the touch was approximately 3 cm/s. For a full description of the task, see Crucianelli et al. (2021).

Immediately after reporting their perception of the reference temperature, the participants were asked to rate their confidence in the accuracy of the response (see Garfinkel et al., 2015). This confidence judgment was reported using a scale from 0 (total guess) to 10 (complete confidence).

To calculate the accuracy, the following formula was applied (from Crucianelli et al., 2021):

$$1 - (\Sigma \frac{(|reported\ temperature - reference\ temperature|)/2}{12})$$

where 12 represents the total number of options presented to the participants (regardless of direction – overestimation or underestimation of temperature) across the three trials. The formula provides a value between 0 and 1, with 0 suggesting poor performance and 1 suggesting optimal performance in the task.

Two variables were introduced: location (palm/forearm) and order of temperature change (increasing/decreasing). For each subject, one increasing value and one decreasing accuracy value for the forearm and for the palm were obtained. To ensure that our analysis was consistent with previous studies showing different skin and central activations for warming and cooling (Hua et al., 2005), we considered the increasing and decreasing trials separately for each skin location.

2.2.3.2 Temperature detection task

The detection of cold and warm static thermal stimuli was measured using the well-established Martsock methods of the limits (Fruhstorfer et al., 1976). We used the same protocol adopted by Heldestad et al. (2010) and Crucianelli et al. (2021). The experimenter kept the thermode on the forearm or palm of the participant without applying additional pressure. Participants were asked to hold a response button in their right hand and to press it as soon as they perceived a change in the temperature in any direction (i.e., warmer or colder than the previously perceived temperature; see Heldestad et al., 2010). The starting point of the stimulation was 32 °C. As soon as the participants pressed the button, the temperature automatically changed in the opposite direction and returned to the baseline temperature, where it stayed for 5 seconds before moving to the next trial. The temperature changed at a rate of 1 °C/s and returned to baseline at a speed of 4 °C/s. Participants completed 5 trials of the task per order (increasing/decreasing temperature), both on the palm and the forearm. Starting the task from the palm or forearm was counterbalanced across participants and sessions.

We did not ask the participants to rate their confidence in the accuracy of response since the task followed a standardized method, which would be disrupted by applying additional measures.

Optimal performance was operationalized as (1) sensitivity to temperature change, i.e., average difference from the target temperature (32 °C), and (2) consistency in perceiving changes in temperature, i.e., standard deviation of the trials within an increasing (warmth perception)/decreasing (cold perception) block for both palm and forearm (for a similar approach, see Crucianelli et al., 2021).

2.2.4 Tactile grating orientation task

The experimental stimuli consisted of eight hemispheric plastic domes with stamped parallel bars and grooves of equal width (JVP [Johnson-Van Boven-Phillips] Spatial Discrimination Domes, Stoelting, Inc. Wood Dale, IL). The different grating widths were as follows: 0.35, 0.5, 0.75, 1, 1.2, 1.5, 2 and 3 mm. The same exact set of gratings was used in several other studies examining the effect of visual deprivation on tactile acuity (e.g., Van Boven et al., 2000; Merabet et al., 2008; Norman & Bartholomew, 2011; Crabtree & Norman, 2014). The right index finger of the subject was fixated on a table in a palm-up position and immobilized using adhesive tape applied to the nail. Gratings were manually applied to the distal pad of the right index finger for ~1.5 seconds, with moderate force. Previous reports demonstrated that these stimuli can be delivered manually because performance in this task has been shown to be independent of subtle changes in time and pressure of application (Van Boven & Johnson, 1994; Johnson & Phillips, 1981; Vega-Bermudez & Johnson, 1999). The orientation of the gratings was placed either horizontally or vertically relative to the long axis of the finger. In each trial, a two-alternative forced-choice procedure was used in which subjects had to verbally report whether the grating was oriented horizontally or vertically. The task was terminated when the subject reached the chance level, i.e., 50% or less correct responses. Every experimental session consisted of up to eight blocks, with one for each grating width. Each block consisted of 20 randomized trials, half with horizontal gratings and half with vertical gratings. The sequence of the blocks corresponded to a decreasing width order of the gratings. Care was taken by a trained experimenter to avoid any movement of the finger during contact with the grating. No feedback about the accuracy of the response was given to the subjects at any time.

Immediately after reporting the orientation of the grating, the participants were asked to rate their confidence in the accuracy of the response (see Garfinkel et al., 2015). This confidence judgment was made using a scale from 0 (total guess) to 10 (complete confidence).

The percentage of correct responses was computed for each block, and the grating orientation threshold was calculated by linear interpolation between grating widths spanning 70% correct responses (see Van Boven & Johnson, 1994; Merabet et al., 2008; Wong et al., 2011a; Garfinkel et al., 2016b). Six participants from the deprived group and 9 participants from the non-deprived group were excluded from the data analysis because they could not complete the majority of the test blocks or could not perform the task beyond the expected level (70% accuracy).

2.3 Data analysis

The data were tested for normality using the Shapiro-Wilk test and found to be not distributed normally ($p < .05$). However, we decided to use parametric tests for all analyses because of their utility in factorial designs and ANOVAs, such as in the current study (see Guterstam, Larsson, Zeberg & Ehrsson, 2019 for a similar approach). The use of non-parametric tests yielded the same results as our parametric approach, which is consistent with the notion that t statistics are reasonably robust to non-normality (Sawilowsky & Blair, 1992; see Supplementary Results). Bonferroni correction was used as a follow-up for significant effects and interactions. All p values were two-tailed. For the Bayesian analyses, the default Cauchy prior was used. For data visualization, raincloud plots in R were used (Allen, Poggiali, Whitaker, Marshall & Kievit, 2019).

3. Results

3.1 Heartbeat counting task

We predicted that in the heartbeat counting task, participants from the deprived group would show significant improvement after blindfolding but that their accuracy would return to the baseline level after the wash-out (light re-exposure) period, while the non-deprived group would not show this pattern of accuracy changes across sessions. However, our results did not support this hypothesis (no main effect of *group*, $F = .039$, $p = .844$, no interaction between *group* and *session*, $F = 1.333$, $p = .267$). Rather, our results revealed that the interoceptive accuracy improved over time, independent of whether the participant had experienced visual deprivation (main effect of *session*, $F = 12.981$, $p < .001$; Figure 2). Thus, no effect of specific blindfolding per se could be established. This conclusion was confirmed by further exploratory analyses: in the blindfolded group, the Bonferroni-corrected post hoc comparisons ($\alpha = 0.017$) revealed a significant difference between sessions I and II (t(31) = –2.838, p = .008; M_1 = .747, SD_1 = .151; M_2 = .800, SD_2 = .122) and no significant difference between sessions II and III (t(31) = .641, p = .526; M_3 = .789, SD_3 = .127). Similarly, in the non-blindfolded group, we found a significant difference between session I and session II (t(31) = –3.147, p = .004; M_1 = .720, SD_1 = .125; M_2 = .790, SD_2 = .146) and no significant difference between session II and session III (t(31) = –.932, p = .358; M_3 = .809, SD_3 = .121). Further exploratory analysis of performance between the groups during each session did not reveal statistically significant differences (session I, session II and session III: t(62) = .783, p = .437; t(62) = .283, p = .778; t(62) = –.633, p = .529, respectively).

To test whether our data provided evidence for the absence of an interaction of group and session, which would support the null hypothesis, we performed a 2 x 3 Bayesian ANOVA. The Bayesian analysis revealed a Bayes factor of 7.072 in favor of the null hypothesis (BF_{01} = 7.072) of no interaction between *group* and *session*, indicating that the data were 7.072 times more likely under the null hypothesis than under the alternative hypothesis. Furthermore, a Bayesian paired t-test run for a direct comparison of S2 between the blindfolded and control groups revealed a Bayes factor of 3.784 (BF_{01} = 3.784) in support of the null hypothesis.

Given that beliefs about or knowledge of the resting heart rate as well as the heart rate itself have been shown to influence the performance of the heartbeat counting task (see the *Introduction*), we decided to run an exploratory analysis examining potential fluctuations in heart rate across sessions. We found no main effect of *group* (F = .020, p = .889) but a significant main effect of *session* (F = 60.238, p < .001), with no *group* x *session* interaction (F = .654, p = .522), suggesting that the heart rate of all participants changed (decreased) significantly throughout the course of the experiment. Then, we ran another exploratory analysis examining whether the average number of reported heartbeats changed across sessions in any of the groups. We found no main effect of *group* (F = .001, p = .982), no main effect of *session* (F = 1.151, p = .320), and no significant interaction between *group* and *session* (F = 2.993, p = .054). Taken together, the improvement in accuracy might be driven by natural fluctuations in heart rate and not by task demands, which is consistent with previous studies (*see Introduction*).

The pattern observed in the accuracy measurements was mirrored by the confidence ratings: we did not observe a main effect of *group* (F = .172, p = .680) or an interaction between *group* and *session* (F = .759, p = .470) but did observe a main effect of *session* (F = 5.634, p = .005; Supplementary Figure 1). These findings show that not only the accuracy but also confidence increased across sessions, regardless of the group, although without any notable effect from the blindfolding procedure.

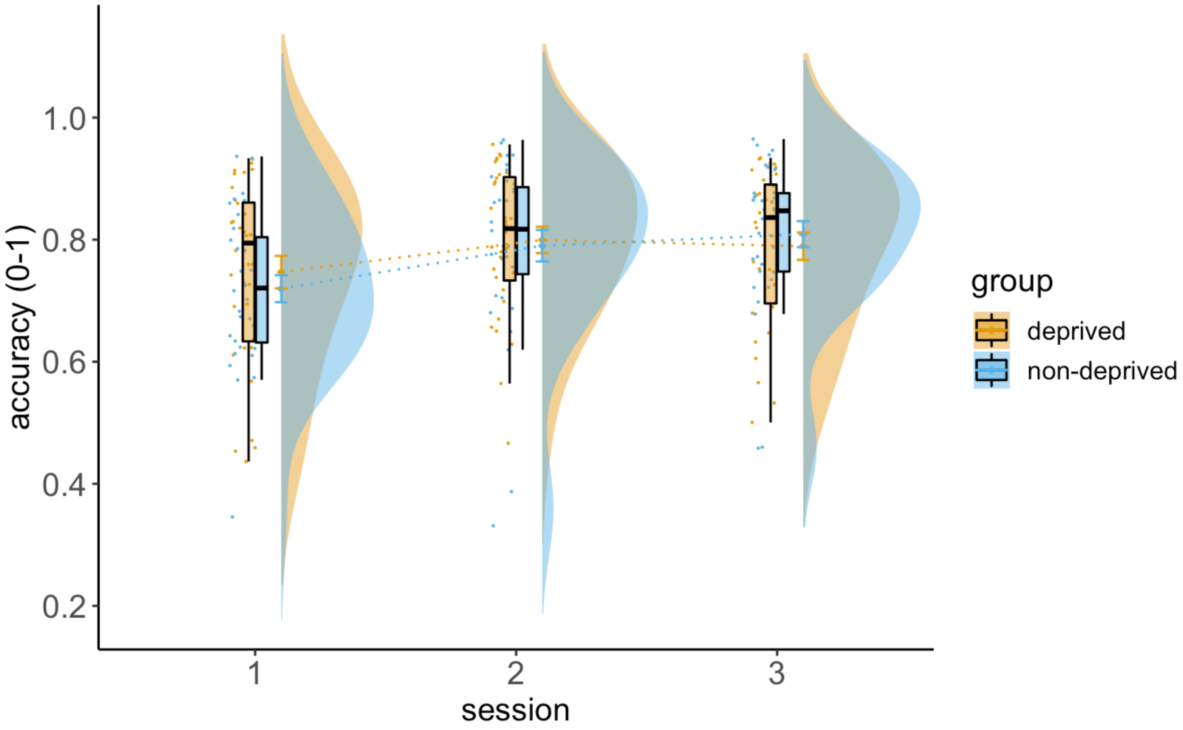

Figure 2. Accuracy in the heartbeat counting task. Individual data points, boxplots, density plots and group means with standard errors are shown. All the following figures are formatted in the same fashion.

The baseline performance in the heartbeat counting task in both groups was comparable with the results obtained in other studies using this paradigm (e.g., Borhani, Làdavas, Fotopoulou & Haggard, 2017), which highlights that the task was successfully implemented in the present study.

3.2 Thermal matching task

We predicted that in the thermal matching task, participants in the deprived group would show significant reversible improvement after blindfolding while participants in the non-deprived group would not show these changes in accuracy across sessions. The analysis of the effect of visual deprivation revealed no main effect of *group* (F = .686, p = .411), although a significant main effect of *session* (F = 3.551, p = .032) and a significant interaction between *group* and *session* (F = 3.502, p = .033; Figure 3) were observed. Bonferroni-corrected post hoc tests ($\alpha = 0.017$) revealed that there was no significant difference in the average accuracy between the groups in any of the sessions (t(62) = 1.886, p = .064; t(62) = –.285, p = .777; t(62) = .542, p = .590 for sessions I, II and III; $M_1 = .839$, $SD_1 = .051$; $M_2 = .836$, $SD_2 = .064$; $M_3 = .844$, $SD_3 = .072$ in the deprived group and $M_1 = .798$, $SD_1 = .110$; $M_2 = .842$, $SD_2 = .097$; $M_3 = .833$, $SD_3 = .099$ in the non-deprived group). However, further Bonferroni-corrected post hoc comparisons ($\alpha = 0.017$) revealed a significant difference between sessions I and II (t(31) = –3.223, p = .003) and no significant difference between sessions II and III (t(31) = .947, p = .351) in the control group. In turn, in the blindfolded group, we did not find a significant difference between session I and session II (t(31) = .226, p = .823) or between session II and session III (t(31) = –.757, p = .455). Taken together, these results suggest that visual deprivation did not significantly influence thermosensation as measured by the thermal matching task.

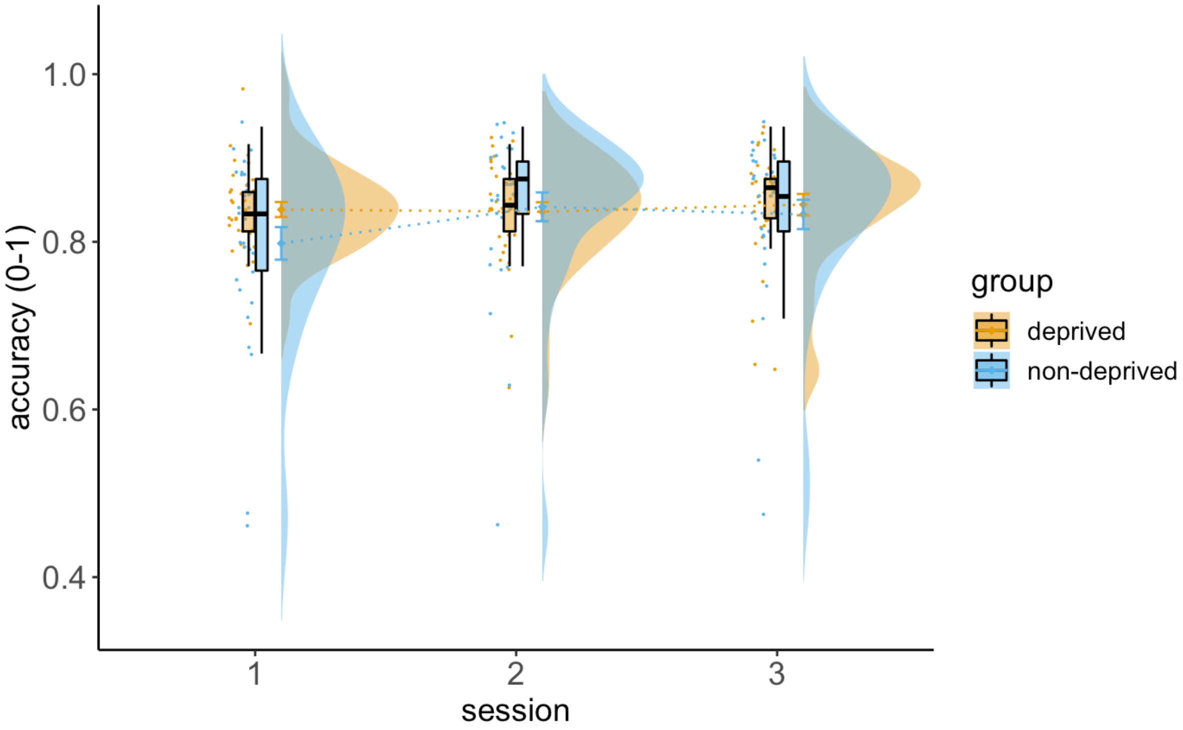

Figure 3. Average accuracy across conditions in the thermal matching task.

In line with Crucianelli et al. (2021), we found that both groups showed higher accuracy in the baseline session when stimulated on the forearm compared to the palm (main effect of *location [arm/palm]*, F = 27.697, p < .001; Supplementary Figure 2). Therefore, we reproduced the basic effect of the thermal matching task on a group with the same number of participants who had similar demographic backgrounds as reported in the original paper of Crucianelli et al. (2021; see *Participants*), which was examined to highlight that the task was successfully implemented in the present study. The analysis of all sessions revealed no interaction between *group* and *location* (F = .730, p = .396) or between *group* and *temperature* (F = .323, p = .572), suggesting that the blindfolding procedure did not influence the *forearm* vs. *palm* difference (Supplementary Figure 3).

In the case of the confidence ratings, we did not observe a main effect of *group* (F = .020, p = .887) or an interaction between *group* and *session* (F = .058, p = .943), and we also did not observe a main effect of *session* (F = .820, p = .443; Supplementary Figure 4), thus showing that confidence did not increase across sessions, regardless of the group. As in Crucianelli et al. (2021), we observed a significant main effect of *location* (F = 21.776, p < .001), with participants being more confident with their answers for the forearm than the palm. We did not observe a main effect of *temperature* (F = 2.266, p = .137) or an interaction between *location* and *temperature* (F = .352, p = .555). Our analyses revealed no interaction between *group* and *location* (F = .700, p = .406) or between *group* and *temperature* (F = .082, p = .776).

3.3 Temperature detection task

As in the thermal matching task (Section 3.2), we predicted that participants in the deprived group would show significant reversible improvement after blindfolding while participants in the non-deprived group would not show these changes in accuracy across sessions. The analysis of the effect of visual deprivation on sensitivity to temperature change revealed no main effect of *group* (F = 1.274, p = .263), no main effect of *session* (F = 1.532, p = .220), and no interaction between *group* and *session* (F = .686, p = .505; Figure 4A).

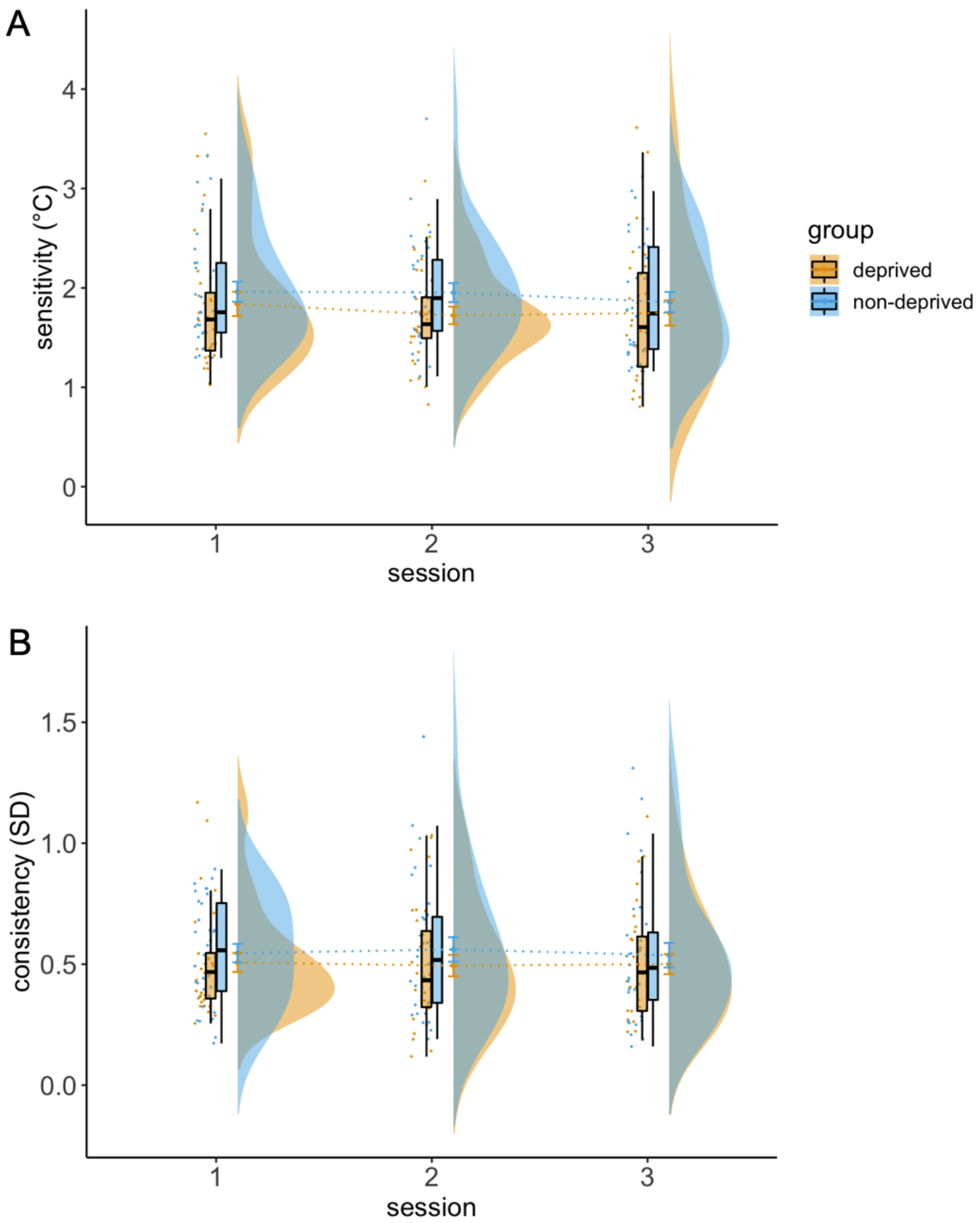

Figure 4. Sensitivity to temperature change (A) and consistency in perceiving temperature change (B) in the temperature detection task.

Similarly, we observed no main effect of *group* (F = .919, p = .341), no main effect of *session* (F = .041, p = .960), and no interaction between *group* and *session* (F =.126, p = .882; Figure 4B) in terms of consistency in perceiving temperature change (Figure 4B).

To test whether our data provided evidence for the absence of an interaction of session and group, which would support the null hypothesis, we performed a 2 x 3 Bayesian ANOVA, separately for sensitivity and for consistency. For sensitivity, the Bayesian analysis revealed a Bayes factor of 8.889 in favor of the null hypothesis ($BF_{01} = 8.889$) of no interaction between *group* and *session*. Similarly, for consistency, the Bayesian analysis revealed a Bayes factor of 9.495 in favor of the null hypothesis ($BF_{01} = 9.495$) of no interaction between *group* and *session*. Therefore, our results suggest that visual deprivation does not influence thermosensation as measured by the temperature detection task.

Additionally, we found that both groups showed higher sensitivity in the baseline session when detecting cooling stimuli compared to warming stimuli (main effect of *temperature*, F = 204.040, p < .001), thereby replicating the effect observed in Crucianelli et al. (2021). The analysis of all sessions revealed no interaction between *group* and *temperature* (F = .007, p = .933) or between *group* and *location* (F = 1.844, p = .179; Supplementary Figure 5).

3.4 Tactile grating orientation task

We predicted that in the grating orientation task, the blindfolded group would show significantly better performance (higher acuity) than the control group in the second session, which will return to the baseline level after light re-exposure, and the control group would not show such changes in accuracy across sessions. However, these predictions were not met. We found no main effect of *group* (F = .110, p = .742), no main effect of *session* (F = 1.628, p = .202) and no interaction between *group* and *session* (F = .120, p = .887; Figure 5). An exploratory analysis of the differences in performance between the groups during each session revealed no statistical significance (session I, session II and session III: t(47) = .001, p = .999;

$t(47) = -.288$, $p = .774$; $t(47) = -.497$, $p = .621$, respectively; $M_1 = 1.463$, $SD_1 = .514$; $M_2 = 1.279$, $SD_2 = .459$; $M_3 = 1.308$, $SD_3 = .554$ in the deprived group, respectively, and $M_1 = 1.463$, $SD_1 = .721$; $M_2 = 1.324$, $SD_2 = .642$; $M_3 = 1.397$, $SD_3 = .703$ in the non-deprived group, respectively). Overall, visual deprivation did not have a significant effect on tactile acuity, and tactile acuity did not improve (or change) over time in either of the two groups.

To test whether our data provide evidence for the absence of an interaction of session and group, which would support the null hypothesis, we performed a Bayesian 2 x 3 ANOVA. Bayesian analysis revealed a Bayes factor of 8.19 ($BF_{01} = 8.19$) in favor of the null hypothesis of no interaction of session and group, indicating that the data were 8.19 times more likely under the null hypothesis than under the alternative hypothesis. Furthermore, a Bayesian paired t-test run for a direct comparison of S2 between the blindfolded and control groups revealed a Bayes factor of 3.386 ($BF_{01} = 3.386$) in support of the null hypothesis. Therefore, our results suggest that visual deprivation does not influence tactile acuity as measured by the grating orientation task.

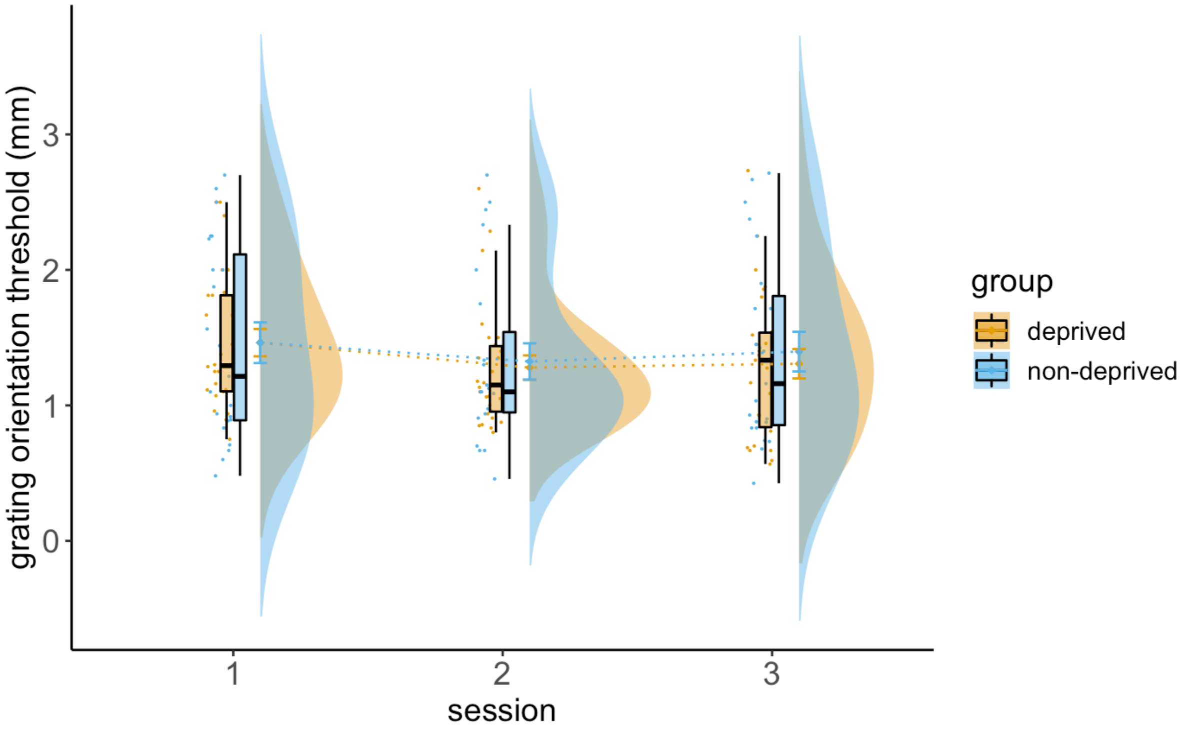

Figure 5. Tactile grating orientation threshold.

The baseline performance in the task in both groups was comparable with the results obtained in other studies using this paradigm (Merabet et al., 2008; Wong et al., 2011; Bola et al., 2016), which highlights that the task was successfully implemented in the present study.

3.5 Relationship across tasks

No significant relationship was found between performance in any of the tasks (Supplementary Table 2). The lack of significant correlations between tasks further supports the idea of independent processing across interoceptive submodalities (in line with Crucianelli et al., 2021; see also Ferentzi et al., 2018).

4. Discussion

In this study, we tested the influence of short-term (110 minutes) visual deprivation in healthy adults on cardiac interoception, thermosensation, and tactile spatial acuity to systematically address the potential influence of visual deprivation on bodily senses through cross-modal plasticity in sighted individuals. Both the deprived and non-deprived (control) groups performed a battery of tasks three times: before and directly after deprivation (or control) and after an additional washout period of 40 minutes, in which all participants were exposed to normal light conditions. We found that both cardiac interoception and skin-based interoception (thermosensation) were resistant to the effects of short-term deprivation, which was confirmed by the observation of the exact same pattern of results in both the classic (static temperature detection task) and newly established (dynamic thermal matching task) thermosensation tests as well as the lack of effect of blindfolding on performance in the heartbeat counting task. We also did not observe a blindfolding-driven change in tactile spatial acuity. Taken together, our results showed no effect on any of the senses tested, suggesting that basic bodily senses are resistant to cross-modal plastic changes induced by short-term visual deprivation.

In a study by Noel et al. (2018) on audiovisual deprivation and cardiac interoceptive accuracy, a very short deprivation period of 15 minutes did not alter interoceptive accuracy in a significant way when considering the whole sample. However, the result of Noel and colleagues might simply be explained by the brief duration of blindfolding because such short periods of visual deprivation have not been shown to lead to any changes on behavioral or neural levels, with 30 minutes being the shortest know deprivation period to produce a reliable effect (Leon-Sarmiento, Bara-Jimenez & Wassermann, 2005). However, why was a period of 110 minutes insufficient to increase the cardiac interoceptive accuracy? One reason could be that the potential sensory enhancements within interoceptive senses are not driven by ‘pure’ cross-modal compensatory plasticity processes but require training periods to be reinforced, which is similar to the tactile improvement observed after very prolonged visual deprivation in blindness (see Alary et al., 2009; Sathian & Stilla, 2010; Voss, 2011; Wong, Gnanakumaran & Goldreich, 2011; for a cardiac interoceptive training example, see Quadt, Mulcahy, Critchley & Garfinkel, 2020). Moreover, Slimani and colleagues (2013) did not find a difference in thresholds for non-painful thermal stimulation between blind and sighted groups, which might suggest that thermosensation is overall resistant to the effects of both short- and long-term visual deprivation, including congenital blindness. In a follow-up experiment, Slimani and colleagues (2014) showed no pain hypersensitivity in late blind individuals, which suggests that enhanced sensitivity to pain following blindness is potentially a result of brain plasticity changes related to early but not late vision loss. Taken together, it could be speculated that some processes ascribed to interoception (e.g., heat pain perception) might be altered only as a result of congenital visual deprivation; moreover, some of these processes (cardiac and thermal interoception) might remain unchanged even under such circumstances, which was further confirmed by the lack of influence of short-term deprivation on the thermal abilities of sighted individuals found in our study.

In keeping with recent research (Wong, Hackeman, Hurd & Goldreich, 2011; Crabtree & Norman, 2014) but inconsistent with the original findings of Facchini and Aglioti (2003), we did not see an improvement in tactile spatial acuity after short-term visual deprivation. Our results follow a number of studies in blind individuals in which improved tactile acuity in blindness were suggested to be mostly driven by experience-dependent mechanisms – for example, increased training of fingertips due to braille reading, and not necessarily by the lack of vision itself (Alary et al., 2009; Sathian & Stilla, 2010; Voss, 2011; see also Wong, Gnanakumaran & Goldreich, 2011).

Interestingly, our negative results in the four bodily tasks examining single modalities were also consistent with recent studies showing multisensory but not unisensory enhancement following short-term deprivation. Fengler and colleagues (2015) did not find any changes in the basic perceptual tasks implemented in their procedure (two unisensory perceptual threshold measures, auditory and visual) but showed a reduced interference effect on multisensory affective prosody judgments. It is worthy to note, however, that multisensory audio-visual discrimination task was not influenced by the blindfolding procedure. Furthermore, in the study of Radziun and Ehrsson (2018), which used a non-visual version of the well-known paradigm of rubber-hand illusion (Botvinick & Cohen, 1998; Ehrsson, Holmes & Passingham, 2005) to probe the dynamic plasticity of body representation, participants from the blindfolded group showed a significantly larger recalibration of hand position sense towards the location of the rubber hand than the control group ("proprioceptive drift"), which is a commonly used behavior index of the illusion. However, the blindfolded group's accuracy in localizing their finger before the illusion, i.e., a unisensory proprioceptive task, showed no significant difference from the control non-deprived group. Similarly, Petkova and colleagues (2012) did not find a difference between blind and sighted participants in a proprioceptive task testing the basic proprioceptive ability to localize their hand in space without vision, although they did observe an altered (abolished) somatic rubber hand illusion in the blind group (Petkova et al., 2012). The spatial recalibration associated with the somatic rubber hand illusion depends on the integration of congruent tactile and proprioceptive signals from the two upper limbs (Ehrsson et al., 2005; Petkova, Zetterberg & Ehrsson 2012), which is a process that can be implemented by sensory integration mechanisms in the frontal and parietal association cortices and the cerebellum (Ehrsson et al 2005). This more complex integration process of bodily signals was specifically affected in both blindfolded (Radziun & Ehrsson, 2018) and blind (Petkova et al., 2012) participants, in contrast to basic proprioception, tactile acuity, or interoception, that presumably rely predominantly on the primary and secondary somatosensory cortex (e.g., Eickhoff et al., 2006; Khalsa, Rudrauf, Feinstein & Tranel, 2009; Haag et al., 2015; Lutz & Bensmaia, 2021) and the insula (e.g., Livneh et al., 2017; Evrard, 2019). The present negative findings also suggest that the previously observed effects of blindfolding on the recalibration of the felt hand position (in the somatic rubber hand illusion; Radziun & Ehrsson, 2018) were due to the altered multisensory integration rather than changes in tactile acuity (i.e., increased sensitivity to tactile incongruence), thermosensation (increased sensitivity to thermal incongruence), or cardiac interoception (Tsakiris, Tajadura- Jiménez & Costantini, 2011, but see also Crucianelli et al., 2018; Horváth et al., 2020). Moreover, multisensory integration within the bodily senses has been shown to be altered in blind individuals, suggesting that visual experiences shape both behavioral and neural responses to tactile–proprioceptive stimulation (Crollen et al., 2017), which again points to the role of vision in multimodal interactions, even when visual input is not directly involved.

Blindfolding in sighted individuals has been shown to modify the excitation/inhibition balance in the visual cortex and lead to increased activation of the visual areas (Boroojerdi et al., 2000; Fierro et al., 2005), which have been reported to become engaged in processing non-visual stimuli (Weisser et al., 2005; Merabet et al., 2007; 2008). Moreover, short-term visual deprivation was demonstrated to be associated with increased excitability of the motor cortex (Leon-Sarmiento et al., 2005); however, the evidence is mixed (Cambieri et al., 2017). Among the investigations of the effects of blindfolding on the brain, electrophysiological studies have shown signatures of improvement of haptic recognition memory (Santaniello, Sebastián, Carretié, Fernández-Folgueiras & Hinojosa, 2018), plasticity of the auditory steady-state response (Lazzouni et al., 2012), and slow-wave changes in cortical visual areas (Bernardi et al., 2019). However, to the best of our knowledge, there are no neuroimaging or electrophysiological studies examining the effects of visual deprivation on active areas and electrophysiological signatures related to cardiac interoception or thermosensation, such as by using the insula as a region of interest. Further studies might throw light on the potential links between various forms of visual deprivation and bodily senses on a neural level.

Importantly, the results of the heartbeat counting task, in which the performance of both groups was compared across three sessions, are consistent with studies highlighting the effect of repeated performance on participants' accuracy (e.g., Ring, Brener, Knapp & Mailloux, 2015). This finding may indicate that the heartbeat counting task is not optimally suited to quantifying cardiac interoception in repeated-measures designs (for a recent debate on the validity of the heartbeat counting task, see: Zamariola et al., 2018; Ainley, Tsakiris, Pollatos, Schulz & Herbert, 2020; Zimpirich, Nusser & Pollatos, 2020; Corneille, Desmedt, Zamariola, Luminet & Maurage, 2020). In contrast, none of the thermal tasks showed an effect of practice on the performance. Thus, thermosensation might provide more stable and robust results regarding the consistency and reliability of participants' performance.

Blindfolding paradigms provide a useful method of inducing and measuring behavioral proxies of neuroplasticity, with the aim of better understanding the rapid plastic changes in the brain. Our work suggests that in cases of cardiac interoception, thermosensation, and discriminative touch, 110 minutes of visual deprivation is not enough to produce any changes on a behavioral level. Further studies might help elucidate why improvement of only some perceptual processes and abilities can be observed after short-term visual deprivation and why basic bodily sensations, such as cardiac interoception, thermosensation, tactile acuity, or proprioception, do not seem to be affected.

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Competing Interests

The authors declare no competing interests.

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