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More than a feeling: Scalp EEG and eye signals in conscious tactile perception

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ABSTRACT

Understanding the neural basis of consciousness is a fundamental goal of neuroscience, and sensory perception is often used as a proxy for consciousness in empirical studies. However, most studies rely on reported perception of visual stimuli. Here we present behavior, high density scalp EEG and eye metric recordings collected simultaneously during a novel tactile threshold perception task. We found significant N80, N140 and P300 event related potentials in perceived trials and in perceived versus not perceived trials. Significance was limited to a P100 and P300 in not perceived trials. We also found an increase in pupil diameter and blink rate and a decrease in microsaccade rate following perceived relative to not perceived tactile stimuli. These findings support the use of eye metrics as a measure of physiological arousal associated with conscious perception. Eye metrics may also represent a novel path toward the creation of tactile no-report tasks in the future.

1. Introduction

One of the biggest challenges in modern science is to understand the neural basis of consciousness (Miller, 2005). Most studies have approached this through the lens of perceptual processing, using a combination of perceptual behavioral tasks coupled with various brain recording techniques, such as scalp and intracranial electroencephalography (EEG), magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI) and direct neural recordings in both humans and animal models (Del Cul et al., 2007; Fukuda & Matsunaga, 1983; Li, Hill, et al., 2014; Pitts, Metzler, et al., 2014; Wyart & Tallon-Baudry, 2008). Although there are several conflicting theories about what gives rise to consciousness itself, studies spanning recording techniques and behavioral paradigms find characteristic activity in sensory areas followed by widespread activity in higher-level associative cortical regions, including frontal and parietal cortices. Studies on visual perception have dominated the field, and although auditory perceptual studies have made inroads, the number of studies examining other senses, including tactile (Al et al., 2020; Auksztulewicz & Blankenburg, 2013;

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Auksztulewicz et al., 2012; Eimer et al., 2003; Forschack et al., 2020; Kida et al., 2006; Schroder et al., 2021; Schubert et al., 2006) and olfaction (Abbasi et al., 2020; Kim et al., 2020) still lags far behind; though, notably, there is an extensive literature on pain perception that stands somewhat apart (Babiloni et al., 2001; Buchgreitz et al., 2008; Douros et al., 1994; Egsgaard et al., 2012; McDowell et al., 2006; Truini et al., 2004). An expanded and rigorous study of the neural basis of consciousness across all sensory modalities is necessary to truly understand whether there are common mechanisms of conscious perception.

The existing literature on somatosensory perception has focused largely on masking or oddball paradigms (Eimer et al., 2003; Kida et al., 2006; Schubert et al., 2006); or studies involving multiple sensory modalities (Eimer et al., 2003; Montoya & Sitges, 2006; Schroder et al., 2021; Schroder et al., 2019). Although these studies provide valuable insight into perceptual processing, such studies almost always present *different* and/or *additional* masking stimuli to control whether a target is perceived. The potential confounds of differences in the stimulus itself begs the question: was the observed brain activity across masked and unmasked conditions different because of the perceptual difference or because of differential stimuli (e.g., two stimuli in a masked condition vs one in an unmasked one)? The use of a threshold detection task eliminates this potential confound, because identical (or functionally identical, as is the case with a perceptual threshold that changes over time) stimuli are presented: only the percept changes. Threshold tasks have been successfully employed in other sensory modalities (Christison-Lagay et al., 2018; Colder & Tanenbaum, 1999; Herman et al., 2019; Kronemer et al., 2021; Pins & Ffytche, 2003; Ress & Heeger, 2003; Wyart & Tallon-Baudry, 2008), and indeed have also been used for a handful of tactile paradigms (Al et al., 2020; Auksztulewicz & Blankenburg, 2013; Auksztulewicz et al., 2012; Forschack et al., 2020; Grund et al., 2021; Palva et al., 2005; Schroder et al., 2021). While these studies have added substantially to our understanding of tactile perception, they also have their own limitations: they either rely on self-reported or two-alternative forced choice reports of perception, which might increase the rate of false alarms or other perceiver-based errors(Al et al., 2020; Auksztulewicz et al., 2012; Forschack et al., 2020; Grund et al., 2021); or in one case, involved a rapid motor behavioral response, which may conflate motor and perceptual components of brain activity (Palva et al., 2005).

Despite these caveats, a picture of the event-related potentials (ERPs) modulated by tactile perception has begun to emerge from previous studies. Multiple studies (Al et al., 2020; Forschack et al., 2020; Forster et al., 2016; Kida et al., 2006; Schroder et al., 2021; Schubert et al., 2006) highlight the N140 as important to perception, although the groups differ slightly as to whether the signal should be interpreted as awareness, perception, detection or attention. Other signals have been implicated in perception and associated tasks. Forster et al. (2016), Kida et al. (2006), and Schubert et al. (2006) suggest that the P100 may be modulated by attention or by conscious awareness; and an increase in the P200 has been related to the needs of complex cognitive functioning such as memory or stimulus evaluation, serving as an index of a stimulus' ability to capture subjects' attention (Forster et al., 2016; Montoya & Sitges, 2006).

While early potentials are often associated with specific sensory modalities, the P300 is commonly reported across modalities. However, despite its prevalence, its interpretation is controversial: it is debated whether the P300 is the result of processes necessary for awareness (Ye et al., 2019) or attention (Pitts, Metzler, et al., 2014), or whether it is the result of post-perceptual processing (Cohen et al., 2020; Koivisto et al., 2016; Kronemer et al., 2021; Muñoz et al., 2014; Railo et al., 2011; Schroder et al., 2021).

Interpretation of electrophysiological signals of perception is further complicated by the use of behavioral report in nearly all perceptual tasks. When subjects are required to report whether or not they have perceived a stimulus, the report itself recruits additional cognitive processes such as the retention of percepts in working memory, the preparation of a motor plan, etc. This poses a particular challenge for perceptual threshold tasks. Although these tasks are very useful in identifying brain activity caused by perceptual differences (as opposed to changes correlated with physically different stimuli), the only difference between trials are, in fact, the participant's perception, which must be read-out in some fashion. Therefore, development of covert measures of conscious perception are particularly important. One promising avenue of study has proposed using pupil diameter, blink, and microsaccade rates to covertly measure changes in physiological arousal, which in turn correlate with changes in cognitive engagement and perception (Dalmaso et al., 2017; Eckstein et al., 2017; Einhauser et al., 2010; Kang & Wheatley, 2015; Kronemer et al., 2021; Laeng & Endestad, 2012; Piquado et al., 2010). As with other methodologies, eye metrics have most frequently been used with visual paradigms; however, isolated studies have shown differences in pupil diameter (Lee & Margolis, 2016; van Hooijdonk et al., 2019), and microsaccade rate (Badde et al., 2020) associated with tactile perception.

Here, we present findings using a novel tactile threshold task, which was conducted with concurrent high-density scalp EEG and eye metric recordings. We find that there are differences in ERPs, pupil diameter, and blink and microsaccade rates between trials with a perceived versus a not perceived stimulus presented at the participant's perceptual threshold. To our knowledge, this is the first time that a tactile threshold task has been performed using both pupillometry and high-density scalp EEG (hdEEG) to help elucidate the underlying mechanisms of consciousness.

2. Materials and methods

2.1. Participants

Twenty-six participants were recruited to participate in the task. From those, 10 participants completed the behavioral task with simultaneous high-density electroencephalography (hdEEG) alone, and 16 with hdEEG collected concurrently with eye metrics. Of these, two participants were entirely excluded from analysis due to poor behavioral performance (lower than 65 % accuracy on finger localization); four were excluded from eye metric analyses due to EyeLink technical failure (e.g., EyeLink was unable to calibrate) and one from hdEEG analysis due to excessive noise contaminating all channels during recording. Data analysis of hdEEG signals was completed for 23 participants (10 male; 6 left-handed); analysis of eye metrics was completed for 10 participants (4 male; 3 left-handed). All experimental procedures were approved by the Yale University Institutional Review Board and all participants provided written informed consent.

2.2. Task design

The behavioral task tested tactile conscious perception using a vibration delivered to the pad of one of the four non-thumb fingers (Fig. 1B). One hand was designated as the stimulus-receiving hand and the other hand as the response hand; hand selection was counterbalanced across individuals. Vibrating tactors (C-2 tactor, Engineering Acoustics, Inc.) were secured to each of a participant's fingers using adjustable foam straps and a custom-made positioning template. Straps were color-coded to correspond to their counterpart button on a four-button response box (Current Designs, Inc) that was controlled by the hand contralateral to the hand receiving

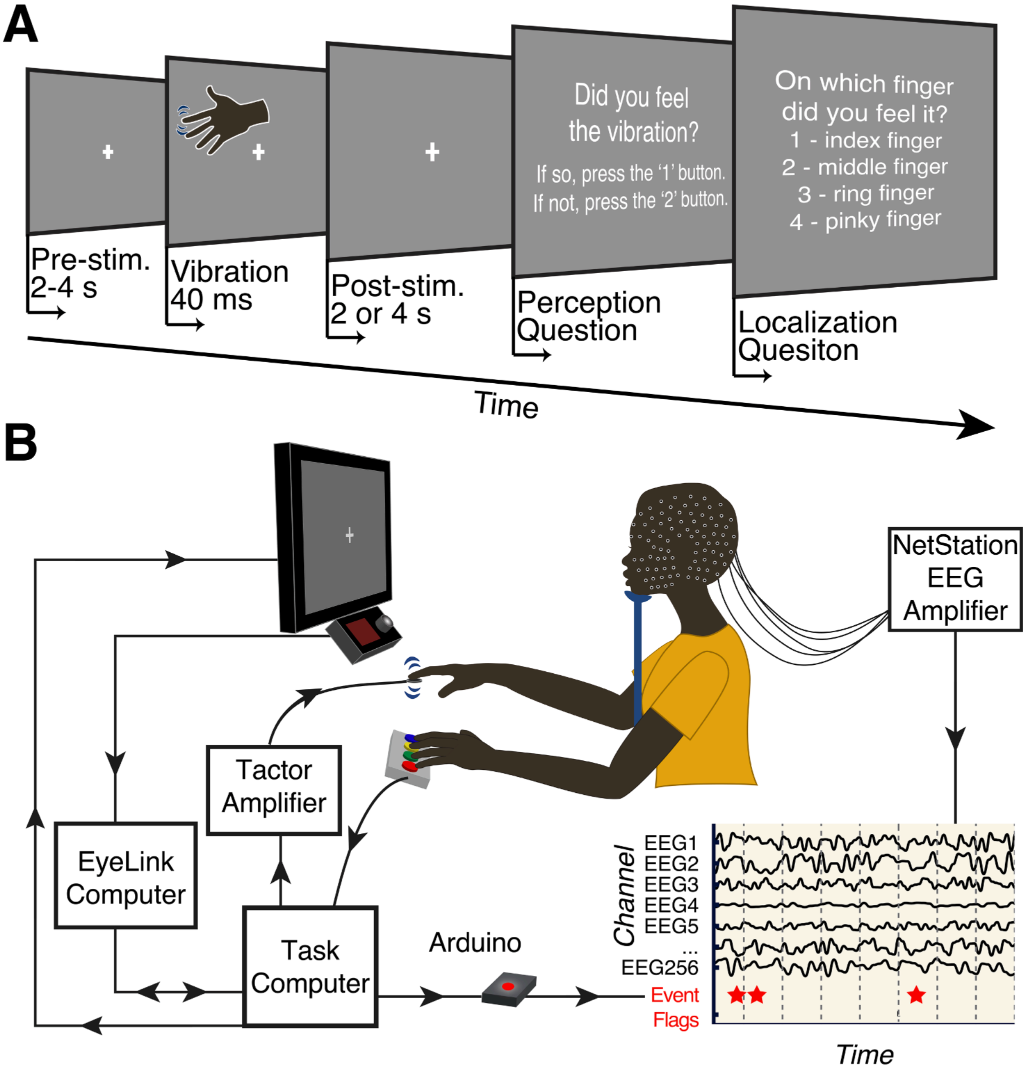

Fig. 1. Tactile threshold task and experimental set-up. (**A**) Threshold tactile task for a single trial. Trials began with a randomly jittered pre-stimulus duration of 2–4 s of a gray screen with a white fixation cross, which was followed by a 40 ms 200 Hz sinewave vibration presented to one of a participant's fingers (index, middle, ring or pinky) at the participant's tactile threshold. After a post-stimulus delay of 2 or 4 s, participants were prompted (on-screen) to answer two forced choice questions regarding 1) whether they felt a stimulus, and 2) to which finger it was delivered. Participants answered with their non-stimulated hand using a response box. The next trial began immediately following button press for the second question; there were a total of 50 trials per run. (**B**) Experimental set up. Participants were positioned in a chinrest (to stabilize head position), facing an external monitor (which showed a fixation cross or task-related questions) and an infrared (IR) camera to record eye metrics. The external monitor was attached to a laptop, which ran the tactile task. Signals for the tactile stimuli (sinewaves generated by the laptop) were sent to an amplifier and then to vibrating tactors that were placed on the participant's fingers. The participant's free hand was used to control a response box that was connected to the laptop. Signals from the IR camera were sent to a dedicated pupillometry computer. Behavioral task, response, and eye metric data were synchronized via an Ethernet connection. Behavioral task, response, and EEG data were synchronized by TTL pulses, initiated by the laptop, and generated through an Arduino, which was recorded directly through the EEG amplifier.

stimuli.

A computer screen, with a central white fixation cross on a gray background, was placed in front of the participant. The distance from the central fixation cross to the bridge of the participant's nose was standardized to 55 cm when eye metrics were measured (85 cm when eye metrics were not measured); the size of the displayed screen was adjusted to keep the apparent size and viewing angle (19° across the horizontal dimension) consistent across conditions.

Pre-test training was conducted to familiarize participants with the stimuli. In this training, participants received suprathreshold stimuli to each finger in turn, and were asked to identify which finger had received stimulation. Following training, participants completed four runs of 50 trials each (200 trials total). For each trial (Fig. 1A), participants were asked to fixate on a white cross positioned centrally on a gray background on the computer screen while they waited for a vibration to be delivered to one of their fingers in random order. Participants were told that they may or may not feel a vibration on every trial. Trials began with a randomly jittered 2–4 s period in which the participant fixated on the white cross on the computer screen. Following this period, a 40 ms, 200 Hz vibration was delivered to one of the fingers in 86 % of trials; 14 % of trials did not have a vibration (blank trials). Stimuli were delivered in random order to the four non-thumb fingers in equal proportions. Following the vibration (or blank), there was an additional 2 or 4 s delay (each occurring 50 % of the time) before the first behavioral report question was presented on the screen. Participants were asked two, self-paced forced-choice questions, presented successively on the computer screen. The first question (perception question) was: "Did you feel the vibration?" which offered two options: 1 for yes, 2 for no; or 2 for yes, 1 for no. The 'yes' button was counterbalanced across participants, but remained constant for the duration of the study for a given participant. Following the perception question, participants were presented with the question (localization question): "On which finger did you feel it?", with the numbers one to four followed by their corresponding fingers (1-index, 2-middle, 3-ring, 4-pinky). Participants were asked this question regardless of their answer to the first question; if they reported not feeling the vibration, they were instructed to answer the second question randomly. Participants reported their answers to these questions using a response box placed under the hand contralateral to the hand receiving stimulation (Fig. 1B). To aid in answering the second question, both the color and finger identity of the button box corresponded to the hand receiving stimulation (e.g., if they felt a vibration on their right ring finger (green strap), they should respond by pressing the button for their left ring finger (green button)). Data were acquired in runs consisting of 50 trials. Each run took an average of 11.65 min, and participants completed a median of 200 trials (range 197 to 250).

2.3. *Experimental design and equipment*

Tactile stimuli consisted of a 200 Hz sinewave pulse (peak sensitivity for Pacinian Corpuscles, (McGlone & Reilly, 2010)) presented for 40 ms. The amplitude of stimulation presented was calculated independently for each finger in a trial-by-trial manner to approximate the participant's 50 % perceptual threshold, using a minimized expected entropy staircase method, which adjusted stimulus amplitude continously throughout testing based on prior recent responses (the MinExpEntStair function included in Psychtoolbox, based on Saunders and Backus (2006)). The task was written in MATLAB (The Mathworks Inc., Natick MA, United States) using the Psychophysics Toolbox ('Psychtoolbox') extensions (Brainard, 1997; Cornelissen et al., 2002; Kleiner et al., 2007; Pelli, 1997). Stimuli were generated in MATLAB, amplified (Marantz NR1609 AV Receiver), and transduced by vibrating tactors (C-2 tactor, Engineering Acoustics, Inc.) placed on the participants' fingers (Fig. 1B).

When eye metrics were measured, participants viewed a fixation cross on a visual display placed directly above a mounted EyeLink 1000 Plus (SR Research, Ottawa, Canada) pupillometer and infrared illuminator. Luminance was controlled across testing sessions by using consistent lighting sources within a windowless testing room. Binocular eye tracking data were collected in head-stabilized mode at 1000 Hz; head stabilization was achieved using a cushioned chin and forehead rest. Prior to the initiation of the behavioral task, participants performed an automated eye-gaze calibration procedure to ensure accurate tracking of eye position.

Non-invasive hdEEG was recorded from the scalp using a 256-channel net (HydroCel GSN 256, Electrical Geodesics, Inc. Eugene, Oregon). Electrodes were placed using SIGNAGEL (VWR International, LLC, Radnor, PA USA) to enhance conductivity between head and electrodes. After gelling the electrodes, the impedance was measured and was considered acceptable if it was $<$70 kΩ in more than 90 % of the electrodes. Signals were amplified through two 128 channel EEG amplifiers (Electrical Geodesics, Inc. Eugene, Oregon), and recorded and digitized via a NetStation System (1000 Hz sampling rate, high-pass filter of 0.1 Hz, low-pass filter 400 Hz). During recording, channels were Cz-referenced; all results were re-referenced to the average of the mastoids in post-processing.

Behavioral task, response and pupillometry data were synchronized using digital timing information sent over an Ethernet connection between the behavioral laptop and EyeLink computer, so that the timing of behavioral events (start of trials, runs and questions; stimulus presentations and button presses) could be recorded on the same time base as the EyeLink recordings. In addition, to ensure precise synchronization between behavioral task, response, and EEG data, TTL pulses from the behavioral laptop were directly input to the EEG amplifier and recorded as event flags on the EEG recording on Netstation. TTL pulses – again corresponding to the start of trials, runs, and questions; stimulus presentations and button presses – were initiated by the laptop (Macbook Pro) running the task and generated by an Arduino Uno (*R*3; Smart Projects) that connected to the digital input port of the EEG amplifier via a DB9 cable. Responses were recorded using a four-button response box (Current Designs, Inc., Model OTR-1x4-L), which was connected to the laptop via USB and sampled by the computer at 1000 Hz.

2.4. *Data analysis*

2.4.1. *Behavioral analysis*

Trials were considered for analysis if they were classified as confirmed perceived or confirmed not perceived, as validated by the location question. Trials in which a vibration was present, reported as felt, and then localized to the correct finger were considered confirmed (validated) perceived; trials in which a vibration was present, reported as not felt, and then incorrectly localized were considered confirmed (validated) not perceived.

Because the tactile perceptual threshold was observed to change across the course of a single behavioral session, a continually adjusting staircase method was used to approximate the instantaneous perceptual threshold. This method results in many trials that are at threshold, but some that are presented at amplitudes supra- and sub-threshold; therefore, a Euclidean distance analysis was used to select trials that were presented closest to the perceptual threshold, and to match the magnitude of confirmed perceived and confirmed not perceived trials used in the analysis. To do so, for each participant, on a finger-by-finger basis, trials categorized as confirmed perceived and confirmed not perceived were selected. The order of confirmed perceived trials was randomized; the shuffled order of confirmed perceived trials was then used to match each confirmed perceived trial's amplitude to the confirmed not perceived trial with the closest amplitude. If the amplitude difference between the confirmed perceived and confirmed not perceived trials fell within 0.03 (arbitrary units [au]; the testing algorithm could adjust in 0.001 au increments), the pairing was included and both trials were removed from their respective pools; if it fell outside of those boundaries, that confirmed perceived trial was discarded and the confirmed not perceived trial was replaced into the confirmed not perceived pool. This continued until all confirmed perceived trials were either paired with a unique confirmed not perceived trial or discarded. The total number of trials included was tallied, and the sum of differences between each unique pairing was calculated. After 100,000 replications of this procedure, the replication with the largest number of trials was retained, and the trails from that replication were selected for analysis. If two or more replications yielded the same number of included trials, the replication with the smallest sum of amplitude differences was selected; if this was also identical, a replication was chosen randomly from the equivalent replications. For simplicity, we will hereafter refer to this selected subset of trials as perceived and not perceived, with the understanding that all analyzed trials have been validated by both localization accuracy (see the preceding paragraph) and proximity to the participant's perceptual threshold (current paragraph).

2.4.2. *Event-Related Potential (ERP) analysis*

After extraction from the NetStation system, the EEG data were analyzed using MATLAB and EEGLAB (Delorme & Makeig, 2004). For each participant, a high-pass 0.1 Hz filter and the CleanLine procedure (Mullen, 2012) were applied to exclude low-frequency drifts and line noise in the 60 Hz and 120 Hz frequency bands. To reject trials with high-frequency noise (e.g., from muscle or movement artifact), high frequency power was calculated using a high-pass 30 Hz filter applied at the channel level across the entirety of the session (window size: 4 s, 2 s overlap). Epochs were identified and cut from −2,000 ms to +2,000 ms, centered on the vibration onset. All further analyses were conducted independently for trials belonging to either perceived or not perceived trials (see 2.4.1). Channels with excessive high frequency power (20 % or more timepoints of the filtered high frequency power in a trial exceeded 100 μV) were excluded, and their positions were re-populated using a spherical interpolation (EEGLAB pop_interp function, there were no more than 10 % of channels deleted in a trial). The resulting data were re-referenced to the average of the mastoids' signals. Epochs were collated and passed through a semi-automatized principal component analysis (PCA) and Independent Component Analysis (ICA) decomposition rejection procedure (EEGLAB pop_runica function utilizing the infomax algorithm for ICA decomposition), in which the ten principal components that explained the most variance of the data were identified, and then among these components 10 independent components were found. Trained study personnel removed independent components that corresponded to signatures for blink, eye-movement, and heartbeat artifacts. Finally, a 25 Hz lowpass filter was applied, and the average of perceived, and not perceived epochs were acquired. To ensure that the 25 Hz filter did not remove important components of the signal we also analyzed the data with a 40 Hz lowpass filter but found no substantial differences aside from introducing additional noise (data not shown), so we chose to retain the 25 Hz filter setting. The resulting signals were baselined by subtracting the mean of the interval from −1000 to −1 ms (the second preceding stimulus).

To control for effects of lateralization, the brain maps of participants that received the vibrations on their left hand were mirrored, with the electrodes assuming the position of their contralateral equivalents. Therefore, for all analyses, the electrodes displayed on the left side of the head represent signals contralateral to the side of the stimulated hand, and electrodes displayed on the right side of the head represent signals ipsilateral to the side of the stimulated hand. After pooling data by first calculating within-participant mean ERPs, the means and SEM were calculated across participants. The results were then resampled at 200 Hz (using MATLAB function imresize). Separate mass univariate analyses (MUA) for perceived, not perceived, and the result of the subtraction (perceived – not perceived) were conducted across all electrodes and timepoints (0 to 1000 ms post-stimulus) using the Mass Univariate ERP toolbox (Groppe et al., 2011). In short, we employed independent t-tests in conjunction with the Benjamini and Hochberg (1995) method of False Discovery Rate (FDR) (as instantiated through the Mass Univariate ERP toolbox, Groppe et al. (2011)) to identify significant areas (electrodes and timepoints). (Benjamini & Hochberg, 1995) FDR was necessary to control for multiple comparisons across electrodes and timepoints by computing the p-values for each timepoint at each electrode, combining, and sorting the entire distribution of p-values, and computing a corrected threshold based on alpha level <0.05. For the P300 peak times, the timepoint with the highest voltage for the Pz electrode was found for the average ERP across participants.

2.4.3. *Eye metrics analyses*

Eye-metric data were analyzed in custom software written in MATLAB. First, to prepare eye-metric data for analysis, artifact rejection was conducted to remove invalid portions of data. Blinks and artifacts were detected by implementing a MATLAB procedure called Stublinks (Kronemer et al., 2021; Siegle et al., 2003). Data segments were flagged if no pupil was detected (due to blink or loss of signal); or if signal spikes were detected (e.g., those associated with the opening or closing of the eyelid during a blink, or those differing more than 4 mm from a trial's median diameter). Segments of flagged data that lasted from 100 to 400 ms were labeled as blinks based on their duration (Schiffman, 2001) and used to generate the blink timecourse data; other flagged segments were marked as artifact. For pupil diameter and gaze (microsaccade) analyses, the rejected samples were linearly interpolated (MATLAB stublink function for pupil data, and naninterp for gaze data) with temporally adjacent samples to restore the omitted time points.

Eye metrics (pupil diameter, blink rate, microsaccade rate) were analyzed as a function of trial type (e.g., perceived or not perceived) on a per participant basis, and then averaged across participants. For each metric, a time window from 1000 ms before the vibration to 2000 ms following vibration onset was extracted and analyzed.

To calculate the mean pupil diameter timecourse, we first baseline-corrected the data to control for changes in steady-state (e.g., not event-related) pupil diameter across runs, or differences across participants. This was achieved by subtracting the median pupil diameter from the 1000 ms preceding the onset of the vibration on a trial-by-trial basis. The mean of the resulting baseline-corrected timecourses was calculated within trial condition (e.g., perceived or not perceived) within each participant; the grand mean across participants was then calculated.

Blink rate, using the detected blinks, corresponds to the proportion of trials that had a blink occurring at a given time point (e.g., if 20 out of 100 trials had a blink occurring during time *t*, the blink rate at time *t* would be 0.2). Blink rate was calculated for each time sample; no binning or baselining was applied. The blink rate was done on a participant level, and then averaged across participants.

Saccades were extracted from the eye tracking data and the ones smaller than one degree (microsaccades) were identified using the algorithm described by Engbert and Kliegl (2003). Microsaccade rate was calculated by quantifying the number of saccades initiated inside a 500 ms moving window (windows were 500 ms and advanced by 1 ms). On a trial basis, the number of microsaccades initiated within a given window were tallied; this was then converted to the rate of microsaccades per second (e.g., if 3 microsaccades were initiated, the rate within that 500 ms window would be 6 microsaccades/second). Mean microsaccade rates were calculated across trials for each participant; these means were then used to calculate a grand mean of microsaccade rate across participants.

Individual subject analyses were completed by omitting the final grand mean step; means and standard deviation (across trials) were calculated for each individual separately.

To calculate when pupil diameter, blink rate, and microsaccade rate significantly differ as a function of perception, we performed a permutation test on the Perceived – Not Perceived data with 10,000 permutations (Kronemer et al., 2021). Timepoints in the original data were considered to have a significant difference between perceived and not perceived conditions if there was a less than 5 % chance of the observation occurring in the permutated data.

3. Results

3.1. Behavioral results

Participants reported feeling a vibration in 59 ± 1 % (mean ± SEM) of trials in which there was a vibration present (close to the expected 50% threshold amount). This remained relatively consistent across the two post-stimulus delays (2 s: 61 ± 1 %; 4 s: 57 ± 2 %); only two participants had significant differences in their percentage perceived as a function of post-stimulus delay (chi-square < 0.05)) (Fig. 2A). Participants reported feeling a vibration on only 8 ± 1 % of the blank trials (Fig. 2A). On average, 86 ± 1 % of the trials reported as felt were also reported in the correct location (Fig. 2B); 27 ± 1 % of trials that were reported as not felt were reported on the correct finger (chance is 25 %). After the Euclidean distance matching analysis (see Methods), an average of 44 ± 8 trials per condition were included per participant for analysis. The average difference of the stimulus amplitude between perceived and not perceived trials after the Euclidean distance analysis matching was relatively small at approximately 3 %, or 0.0045 arbitrary units (au;

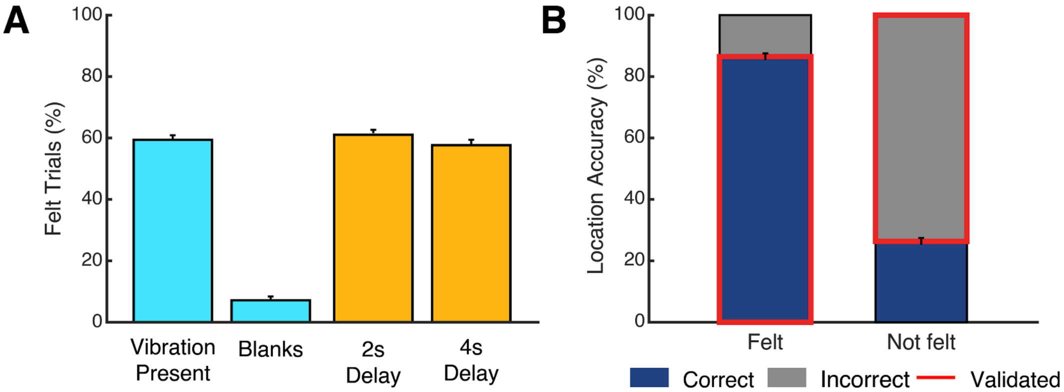

Fig. 2. Behavioral results (n = 23 participants). (A) Responses to perception question. In trials in which a vibration was present, 59 % were reported as felt; in trials in which no vibration was played, only 8 % were reported as felt. Report of vibration was approximately the same for 2 or 4 s post-stimulus delays. Error bars are standard error of the mean (SEM). **(B)** Responses to location question. When vibrations were reported as felt, participants correctly reported which finger received a vibration for 86 % of trials; when they reported they did not feel a vibration (in trials when there was a vibration present), they reported the finger incorrectly for 73 % of trials (chance = 75 %). Correctly identified trials are shown in navy blue; incorrectly identified trials are shown in gray. Data considered for analysis are highlighted in red. Error bars are SEM.

mean amplitude perceived: 0.1251 au; mean amplitude not perceived: 0.1296 au; stimuli ranged from 0.003 au to 0.5 au with 0.001 au increments).

3.2. Evoked potentials

At early times, a brief N80 can be seen reaching significance ($q < 0.05$) at 75 ms post stimulus in one electrode posterior to F7 for perceived and at FP1 for the difference between perceived and not perceived (Fig. 3). Notably, although it does not reach significance, a similar early negative deflection is apparent in most frontal and central electrodes bilaterally for perceived trials. A prominent N140 was observed bilaterally in frontal areas for perceived trials with a somewhat delayed peak at approximately 185 ms after the stimulus, most prominent in the F3 region (Fig. 3). It reached significance ($q < 0.05$) for both perceived analysis alone and when comparing the difference between perceived and not perceived trials. For the not perceived condition, a significant ($q < 0.05$) P100 was found bilaterally in parietal and occipital areas (Figs. 3 and S1). Significant findings remain the same when the data were not mirrored (i.e., when stimulated hand was not controlled for; see S2). In addition, because we excluded many trials based on the stimulus amplitude matching and finger localization criteria, we repeated the analysis without amplitude matching and without regard to finger localization and found generally similar trends in ERPs, although the perception-related N140 was smaller (data not shown).

At later times, significant P300 responses were found for both perceived and not perceived trials; however, the spatial extent, duration, and magnitude were larger for perceived trials (Figs. 4, S1). For perceived trials, the P300 reached peak at 290 ms post-vibration onset, but showed significance above baseline from 260 to 855 ms post-vibration. In contrast, the P300 for not perceived trials has an overall peak at 440 ms (Figs. 4, S1).

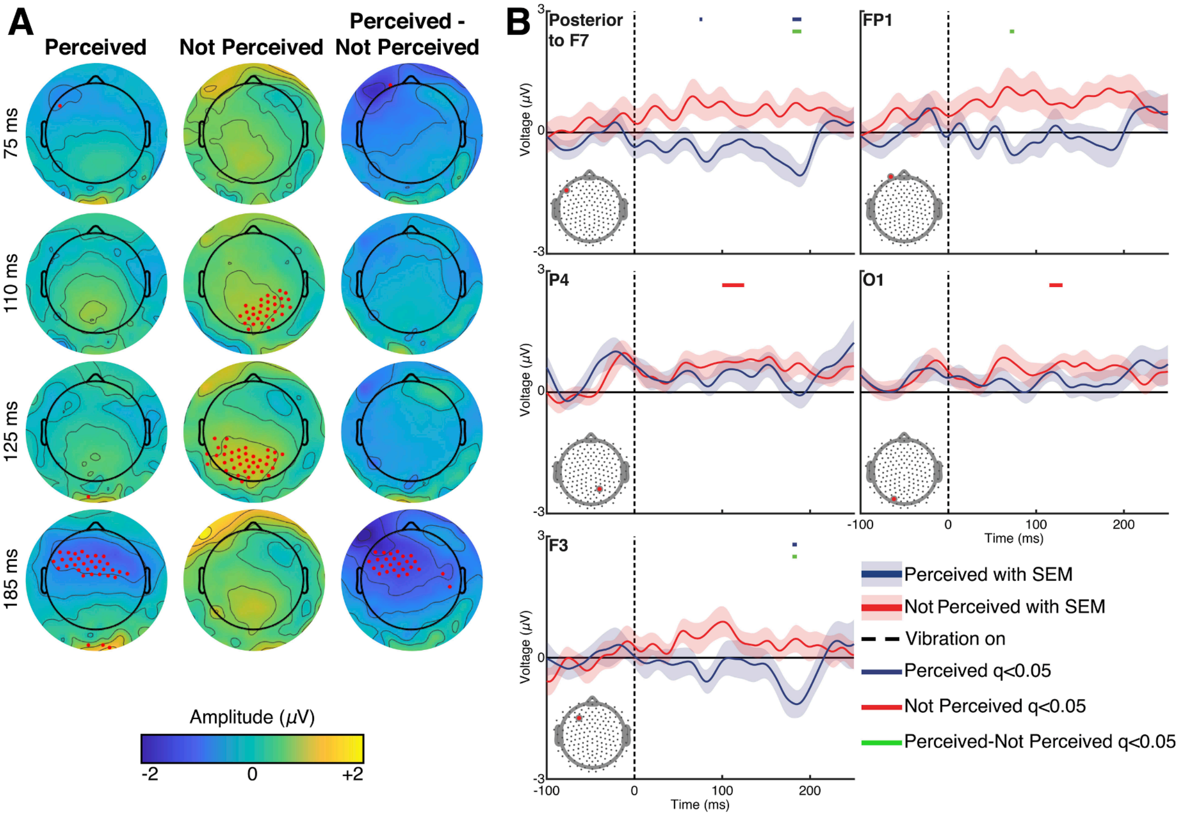

Fig. 3. Early ERPs (n = 23 participants). (A) Voltage topographic maps for early ERPs. Electrodes that achieve significance using independent t-tests with FDR correction (data analyzed: 0 to 1000 ms post vibration, null hypothesis: voltage = 0 μV, $q < 0.05$) are highlighted in red. Times are relative to vibration onset, and were chosen to highlight specific signals of interest (see Fig. S1 for maps at all times). (**B**) Voltage timecourses highlighting early changes post-vibration (-100 ms to + 250 ms from vibration onset). Electrode positions are indicated via a red marker on the map on the bottom left corner of each plot. Blue traces show timecourses of perceived trials; red traces show timecourses of not perceived trials. Shaded error bars show respective SEMs. Red, blue, and green lines at the top of each plot indicate windows that reached significance using independent t-tests with FDR correction. Blue corresponds to significant windows in perceived data; red for not perceived data; and green for the perceived-not perceived data. Times are relative to the onset of vibration, represented by the vertical dotted line.

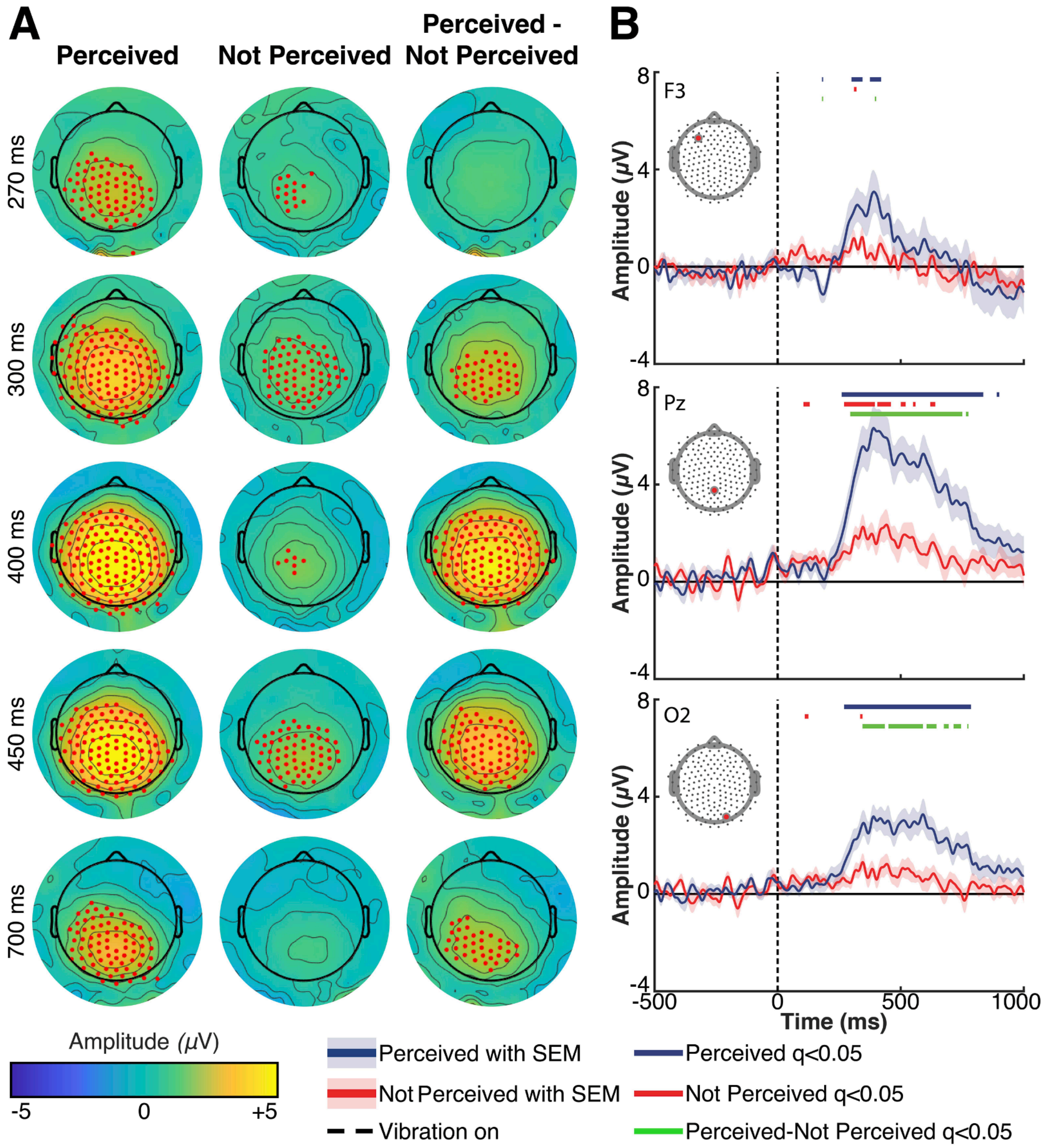

Fig. 4. Late ERPs (n = 23 participants). (**A**) Voltage topographic maps for late ERPs. Electrodes that achieve significance using an independent t-tests with FDR correction (data analyzed: 0 to 1000 ms post-vibration, null hypothesis: voltage = 0 μV, q < 0.05) are highlighted in red. Times are relative to vibration onset, and were chosen to highlight specific signals of interest (see Fig. S1 for maps at all times). (**B**) Voltage timecourses highlighting late changes post-vibration (-500 ms - +1000 ms post-vibration onset). Electrode positions are indicated via a red marker on the map on the top left corner of each plot. Blue traces show timecourses of perceived trials; red traces show timecourses of not perceived trials. Shaded error bars show respective SEMs. Red, blue, and green lines at the top of each plot indicate windows that reached significance using independent t-tests with FDR correction. Blue corresponds to significant windows in perceived data; red for not perceived data; and green for the perceived-not perceived data. Times are relative to the onset of vibration, represented by the vertical dotted line.

3.3. *Eye metrics*

Significant differences were found between perceived and not perceived conditions for pupil diameter, blink rate, and microsaccade rate. Pupil diameter increased markedly for perceived trials, peaking on average approximately 1100 ms following a perceived vibration (Fig. 5A). Pupil diameter was significantly different between perceived and not perceived trials from ~270 ms after vibration to the end of the analyzed epoch (2000 ms post-vibration onset). Blink rate also increased following a vibration for perceived trials, reaching a peak rate ~800 ms post-vibration. Blink rate differed significantly between perceived and not perceived trials for most of the period from ~500 ms post-vibration to the end of the analyzed epoch (Fig. 5B). While pupil diameter and blink rate showed an increase for perceived trials relative to not perceived trials, the microsaccade rate dynamic was more complicated: microsaccade rate

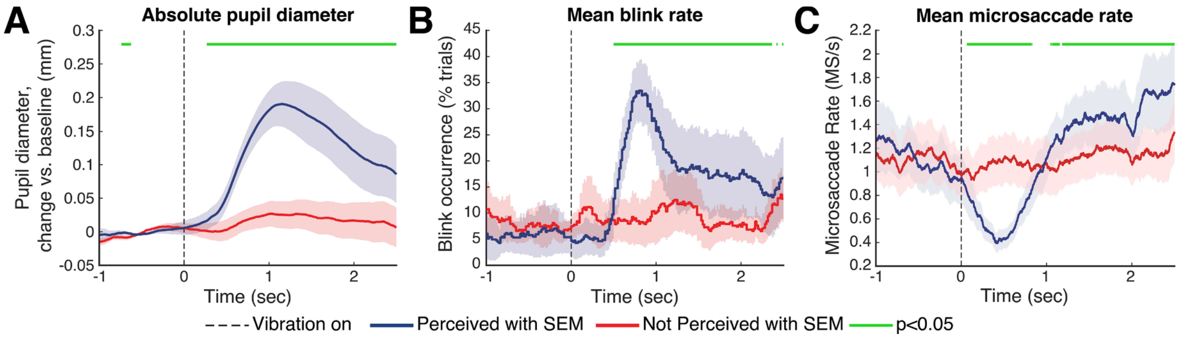

Fig. 5. Eye metrics (n = 10 participants). Timecourses of (**A**) average pupil diameter (**B**) mean percentage of trials where there is a blink occurrence; and (**C**) mean microsaccade rate per second (MS/s). Blue traces represent the grand mean of perceived trials; red traces represent the grand mean of not perceived trials. Shaded error bars show respective SEMs. Times for which there is a significant difference between perceived and not perceived trials are indicated by the green line at the top of each plot. Times are relative to the onset of vibration, represented by the vertical dotted line.

was suppressed in perceived trials relative to not perceived trials from ~250 to 1000 ms post-vibration; but then significantly increased above not perceived microsaccade rate from 1250 ms post-vibration until the end of the analyzed epoch (Fig. 5C). The population level results are recapitulated on the individual participant basis (see S3).

4. Discussion

In this study, we investigated the ERP and eye metric correlates of tactile conscious perception using mechano-vibrational stimuli in a threshold task. For perceived stimuli, we found significant ERPs corresponding to the N80, N140 and P300; for not perceived trials, we observed significant ERPs for the P100 and P300. We also found a significant N140 and P300 when comparing the difference in signals between perceived and not perceived trials (Figs. 3 and 4, S1). Finally, we noted an increase in pupil diameter and blink rate, and a decrease in microsaccades following perceived vibrations (Fig. 5).

Overall, our ERP findings are consistent with the existing literature. The largest signal we observe, the P300 (found in this study starting ~260 ms and lasting until 855 ms) is widely reported, though its interpretation controversial. The P300 has been variously attributed to allocation of attentional resources (Donchin & Coles, 1988; Muñoz et al., 2014), awareness and conscious perception, or to perceptual report or post-perceptual processing (Cohen et al., 2020; Dehaene & Changeux, 2011; Del Cul et al., 2007; Kronemer et al., 2021; Pitts, Padwal, et al., 2014). Although it has historically been considered a marker of consciousness, multiple studies using a variety of paradigms have more recently shown that the P300 is sometimes absent in the absence of perceptual report or when a suprathreshold stimulus is not task-relevant (Cohen et al., 2020; Derda et al., 2019; Kronemer et al., 2021; Pitts, Metzler, et al., 2014; Pitts, Padwal, et al., 2014; Polich, 2007; Railo et al., 2011; Ye et al., 2019). Notably, our task does require perceptual report — even in the absence of a vibration or perception, and so it is interesting to note that we observe a P300 in both perceived and not perceived trials. However, the amplitude and spatial extent of the P300 is greater for perceived trials. These findings are the tactile equivalent of findings by Pitts, Metzler, et al. (2014), Pitts, Padwal, et al. (2014) who, in a visual backward masking task, found a P300 (P3b) in not perceived trials. Like our findings, they report the P300 for not perceived trials had a smaller amplitude than the one found for perceived trials. They concluded that the P300 is likely to reflect post-sensory, or attention-based processes necessary for completing a task, but it may not be a marker for conscious perception itself. Similarly, Schroder et al. (2021) report that the P300 was modulated by choice, the probability of detection, and by intensity of stimuli. Our findings support these interpretation: we posit that the P300 is related to post-sensory processes—which is to say, post-stimulus processing, but not necessarily conscious perception—and do not believe that the presence of the P300 is a marker that that conscious perception has occurred. However, the relative amplitude of the P300 may, indeed be modulated by processes that are at least conscious-perception adjacent.

Some might argue that because Schroder et al. (2021) used a combination of visual and tactile stimuli, and because Pitts, Metzler, et al. (2014) modulated conscious perception through task-relevance, that their interpretation of the P300 as post-sensory processing somewhat independent of conscious access might be suspect, as differential stimuli were used across conditions. However, our task used only tactile target stimuli and they were always task relevant—and we still found the P300 for not perceived trials. Moreover, we presented stimuli at jittered times, so our findings cannot be ascribed to anticipatory effects. Therefore, we feel that our findings substantially strengthen the interpretation of the P300 as a marker associated with post-sensory processing, regardless of conscious perception. Another possible interpretation of the presence of a smaller P300 even without reported perception is that this could arise from incorrectly labelled trials, such as those where participants faintly detected the target but were unable to localize it, or were more generally unsure and therefore reported it as not felt.

The other signals we observed also have precedence in perception literature. Previous studies have shown the N80, P100 and N140 in relation to perceived or salient stimuli (Auksztulewicz & Blankenburg, 2013; Kida et al., 2006; Schubert et al, 2006); however, we do observe the N80 in frontal areas instead of more centro-parietal areas as has been previously reported (Auksztulewicz & Blankenburg, 2013; Schubert et al., 2006). Notably, our results differ from those of Schubert et al. (2006), who suggest that the P100 marks the emergence of perception for a perceived stimulus; we find a P100 for not perceived (and it did not reach significance for our perceived trials), and thus our data is inconsistent with the attribution of the P100 as simply a marker of positive perceptual status.

Dembski et al. (2021) suggest that the N140 negativity is the somatosensory equivalent to the visual and the auditory awareness negativity (VAN and AAN respectively), and that these negativities, collectively, should be considered a main marker of consciousness. However, there is some variability about the interpretation and localization of a negativity occurring at ~140 ms post-stimulus across studies. Dembski et al. (2021) hold that because the VAN and AAN are localized to their respective primary processing areas, the somatosensory awareness negativity (SAN) should be similarly located. This is supported by the findings of Auksztulewicz and Blankenburg (2013), Forster et al. (2016), Forschack et al. (2020) (who calls it N150) and Schroder et al. (2021) who each find a central-contralateral negativity between 100 and 200 ms. Notably, Forster et al. (2016) interpret their N140 as a measure of spatial attention, not awareness; though, notably, their study was not designed to test conscious awareness. In contrast, Schubert et al. (2006) report the N140 bilaterally in frontal (not central) electrodes, but also suggest that it is linked to conscious awareness and is modulated by spatial attention. Our N140 is observed bilaterally in frontal-central electrodes — like Schubert et al. (2006) — but with somewhat greater involvement of contralateral locations. As the N140 is significant for perceived trials, and when comparing perceived to not perceived trials, we suggest that it should, indeed, be considered a marker of conscious awareness. The greater involvement of contralateral electrodes may be due to the allocation of spatial attention to the stimulated hand, and therefore is also in potential agreement with Auksztulewicz and Blankenburg (2013), Forster et al. (2016), Forschack et al. (2020), and Schroder et al. (2021). Also of note is that our 'N140′ peaks around 185 ms. We believe this peak is delayed by ~40 ms from what is often reported in the literature because of the nature of our stimuli: specifically, it is approximately 40 ms longer than other studies (40 ms long, compared 200 μs by Auksztulewicz and Blankenburg (2013), Auksztulewicz et al. (2012), Forschack et al. (2020), Schroder et al. (2021).

A fundamental challenge of conscious perception research is distinguishing brain activity associated with pre- or post-perceptual processing—including perceptual report. The need to disambiguate perceptual report, specifically, from perception is the center of field-wide divisions on theories of consciousness. Indeed, the interpretation of what the P300 represents hinges partially on whether it is a marker of consciousness or a result of report. To remove the potential confounds of using either differential stimuli (such as masks), recent work has explored eye metrics as a covert measure of perception that may open the door for the development of no-report paradigms (Babiloni et al., 2001; Cohen et al., 2020; Derda et al., 2019; Donchin & Coles, 1988; Egsgaard et al., 2012; Koivisto et al., 2017; Koivisto et al., 2016; Muñoz et al., 2014; Pitts, Metzler, et al., 2014; Pitts, Padwal, et al., 2014; Polich, 2007; Railo et al., 2011; Truini et al., 2004).

Although eye metrics – especially pupil diameter – are widely used in visual perception studies (Aminihajibashi et al., 2020; Aston-Jones & Cohen, 2005; Choe et al., 2016; Eckstein et al., 2017; Geng et al., 2015; Kronemer et al., 2021; Otero-Millan et al., 2011; Wang et al., 2017) and in some auditory ones (Wetzel et al., 2016; Zekveld et al., 2018), studies using tactile stimuli are still scarce (Gusso et al., 2021). To our knowledge, there are no prior reports of eye metrics in threshold tactile perception tasks; and in most other tactile studies, stimuli were delivered manually (Iriki et al., 1996; van Hooijdonk et al., 2019) or used recording systems with a sampling rate that, according to Holmqvist et al. (2011), is insufficient to capture nuanced physiological changes occurring at the eye-level (Bertheaux et al., 2020; Ganea et al., 2020; Iriki et al., 1996; Lee et al., 2020; Lee & Margolis, 2016; Schriver et al., 2018; Schriver et al., 2020; van Hooijdonk et al., 2019). The ideal sampling rate for eye metrics, especially if microsaccades are to be measured, is $\gg$ 250 Hz; no mathematical method defines a cut-off value, but it instead has been established through consensus in order to be able to acquire all physiological changes occurring on the eye-level (Holmqvist et al., 2011).

We could not find studies associating blink rates to tactile stimuli. However, previous studies have shown that blink rate is inversely related to cognitive or attentional demand: blink rate decreases with increased attention, and increases when attentional or cognitive demands are removed (Fukuda & Matsunaga, 1983; Siegle et al., 2008). The increase in blink rate immediately following a perceived vibration is consistent with these findings; once a vibration has been felt, the participant has 'achieved' their goal and no longer needs to closely attend to the trial.

Microsaccades have been associated with visual accommodation and a necessary physiologic response so we can process the visual world (Otero-Millan et al., 2011). Here, we show that in addition to being affected by visual paradigms, changes in microsaccade rate can be elicited by tactile perception—notably, by a decrease in microsaccades after perception. This decrease in rate is consistent with a recent study from Badde et al. (2020), who reported oculomotor freezing after cue acquisition. Although our study does not use cues, both Badde et al. (2020) and our current findings are consistent with decreased involuntary eye movement after a perceived sensory event, independent of that event's modality.

The pupil, blink and microsaccade changes we observed with the tactile threshold perception task were very similar to those recently reported for a similarly-designed visual threshold perception task (Kronemer et al., 2021). The consistency of eye metrics in perceptual tasks across sensory modalities, now also encompassing tactile perception, lends further support to the idea that eye metrics serve as a robust covert measure of electrophysiological changes associated with cognitive engagement and its associated changes in physiological arousal levels. The similarity of eye-metric dynamics across sensory modalities and paradigms suggests that eye metrics represent a potentially powerful tool for gauging perceptual and cognitive processing in the absence of overt perceptual report. This approach has recently been applied successfully to conscious visual perception (Kronemer et al., 2021). We plan to leverage these metrics in the development of no-report paradigms in future studies across sensory modalities.

Several of our observations beg further scrutiny. One such finding pertains to the use of both handed participants. Li, Chen, et al. (2014) found that brains from left-handed and right-handed people have different anatomical connectivity, which could affect functioning and lateralization. Therefore, it will be important in future studies to use only participants with either right hand dominance (who show more consistent lateralization of function); or to compare participants with both handedness, coupled with an explicit measure of lateralization. Future studies should also specifically examine how different stimulus amplitudes (threshold vs reliably suprathreshold) affect both ERPs and eye dynamics. Further, although our current paradigm is designed such that there is a dearth of incorrect detection trials (i.e. blank trials reported as perceived, or trials that are reported as perceived and incorrectly identified), a modified paradigm to exploit these trials would allow for comparison of brain and eye dynamics for trials that were confirmed as perceived versus when a participant *thought* they had perceived something. Future studies should explore whether there is a hierarchical relationship (temporally or in terms of magnitude of ERPs) between electrodes that achieve a significant P300 when the stimulus was perceived vs not. Although the recordings were done on a very different scale, de Lafuente and Romo (2006) found a bottom-up correlation with the perceptual experience in single-unit recordings from sensory and frontal cortices in monkeys performing a tactile detection task, and it would be interesting to examine if similar dynamics can be observed at the level of ERPs.

5. Conclusions

Overall, our current study uses a novel tactile threshold paradigm combined with high-density scalp EEG, pupillometry and eye-tracking. We report, using a tactile-threshold task, that ERPs similar to those often associated with perceived stimuli in other sensory domains, such as the N140 and P300, are elicited by perceived tactile stimuli. We note that the P300 (of lower amplitude) is also elicited in our not perceived trials, further complicating the already complex story of what the P300 may represent. We also present data demonstrating that pupil diameter, microsaccade rate, and blink rate differ in a tactile threshold perception task, which suggests that eye metrics may represent a path toward the creation of tactile no-report tasks in the future.

CRediT authorship contribution statement

Mariana M. Gusso: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Visualization. **Kate L. Christison-Lagay:** Conceptualization, Methodology, Software, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **David Zuckerman:** Investigation. **Ganesh Chandrasekaran:** Investigation. **Sharif I. Kronemer:** Methodology, Formal analysis, Writing – review & editing. **Julia Z. Ding:** Formal analysis. **Noah C. Freedman:** Formal analysis. **Percy Nohama:** Methodology. **Hal Blumenfeld:** Conceptualization, Methodology, Resources, Data curation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.concog.2022.103411.

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