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Sensory adaptation is a feature-specific modulation of neural responses and is potentially fundamental to maximizing perceptual sensitivity. Despite its function being unclear, it has been hypothesized that sensory adaptation modifies the neurons' response codes, increasing the ability to process sensory signals on a larger scale. To better understand how such flexibility of our brain is possible, we investigated the effect of high- and low-frequency vibrotactile adaptation on perceived tactile temporal frequency during childhood, a time known for the brain to experience varying levels of plasticity. We tested tactile temporal frequency discrimination thresholds in both children and adults before and after tactile adaptation. Our results demonstrate that sensory adaptation does not consistently change perceived tactile temporal frequency in younger children as it does in adults, as adult-like trends begin to emerge at around 8 years of age but consolidate only in 10-year-old children. The absence of adaptation aftereffects suggests that, under certain conditions, sensory history does not affect perception in younger children in a similar way to adults. Surprisingly, younger children proved to be less flexible in modulating neural responses after prolonged exposure to an adapting stimulus, a tendency conflicting with the high plasticity levels the brain experiences during the early stages of life.

Keywords: sensory adaptation, sensory development, haptics, psychophysics

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Both perception and neurons' responses are significantly affected by sensory history. Shortly timed changes induced by physical events, occurring within the range of milliseconds to minutes, are often referred to as adaptation aftereffects. From a psychophysical perspective, prolonged exposure to repetitive stimulations (i.e., the adaptor) produces profound biases in perception (i.e., adaptation aftereffects). Maybe the most classical example of sensory adaptation is the waterfall illusion, for which repeatedly looking at the flowing flux of the waterfall leads to the impression that the surrounding stones are moving up (Anstis et al., 1998). In general, adaptation aftereffects have been observed in virtually all sensory modalities (Crommett et al., 2017; Goble & Hollins, 1993, 1994; Kohn, 2007; Thompson & Burr, 2009; Wilson, 2000) and have been related to numerous perceptual features (Burr & Ross, 2008; Campbell & Maffei, 1971; Carandini & Ferster, 1997; Domenici et al., 2021; Heron et al., 2012; Jeffery et al., 2010; Tonelli et al., 2017, 2020; Webster & Macleod, 2011).

At the perceptual level, it is assumed that adaptation develops in order to refine perceptual estimation around the adapter's magnitude (Abbonizio et al., 2002; Blakemore et al., 2010; Goble & Hollins, 1993, 1994; Stocker & Simoncelli, 2005), even though there is evidence that adaptation can optimize sensitivity for a wider set of perceptual ranges (Gepshtein et al., 2013). Still, it is surprising to realize how our perception can be shaped by adaptation, considering that perceptual systems can maintain stable representations of the environment even in noisy conditions (Burr & Morrone, 2010).

At the cortical level, it has been suggested that sensory adaptation modifies the neurons' response codes, increasing their ability to process sensory signals within a larger scale (Müller et al., 1999) and optimizing information transmission (Wainwright, 1999). This process should allow for increased coding efficiency (Blakemore et al., 2010). Different theoretical explanations have been given to justify sensory adaptation at a neural level, including metabolic cost reduction (Laughlin et al., 1998) and constant remapping of dynamic range (Fairhall et al., 2001). Unfortunately, none of these theories succeed in providing a widely accepted interpretation of sensory adaptation (Seriès et al., 2009).

Despite the vast amount of literature around sensory adaptation, its neurophysiological mechanisms have mainly been explored through computational (Todorov et al., 1997) or animal models (Carandini & Ferster, 1997; Chung et al., 2002; Connelly et al., 2015; Swadlow &

Gusev, 2001; Temereanca et al., 2008). Nevertheless, here we propose another approach to investigate sensory adaptation based on how it evolves during development, given that childhood is a period known for displaying diverse levels of maturity and plasticity in the brain. To this goal, we tracked the effect of high- and low-frequency vibrotactile adaptation in children, starting from 6 years of age to adults.

Perceived tactile temporal frequency was measured before and after adaptation, using a paradigm previously developed to investigate tactile aftereffects in adults (Watanabe et al., 2010), which was adjusted for the purposes of this study. Notably, while vibrotactile adaptation itself has been highlighted at various levels of information processing (Bensmaïa et al., 2005; O'Mara et al., 1988), the only significant evoked firing covariation with behavioral performance was found considering the primary somatosensory cortex, S1 (Salinas et al., 2000). Therefore, changes in observed performance across age groups should identify different cortical modulations at the S1 level. Tracking adaptation aftereffects at different ages aimed to shed light on how perceptual systems organize sensory information throughout childhood. The results of our current work highlighted that sensory adaptation, overall, is not fully functional at all stages of life but instead—at least for the sensory modality and the perceptual features involved—emerges at around 8 years of age and stabilizes only at 10 years of age.

Method

Participants

A total of 119 participants (105 children and 14 adults) took part in the study. Participants were divided into six groups based on their age (number of participants per group, average, and standard deviation of their age are reported in Table 1). Adults were recruited through the mailing list of the Italian Institute of Technology in Genova, Italy, while children were recruited from two local primary schools in Genova. The total sample size was determined via a priori power analysis conducted using the G*Power v. 3.1.9.7 software (Faul et al., 2009): we found that for a fixed η_p^2 of .06 (medium effect), an α of .05, and a power of .95 there is a 95.2% chance of correctly rejecting the null hypothesis of no significant effect of the interaction with a total sample size of 84 participants (14 per age group). Data were collected at the Italian Institute of Technology, in Genova, in a quiet room specifically used for the collection purpose. All participants reported normal tactile sensibility and no history of neurological diseases or learning disabilities. All testing performances were performed in compliance with the ethics committee of the local health service (Comitato Etico ASL 3 Genova) and the declaration of Helsinki. All adult participants and the legal representatives of the children gave written informed consent to participate in this study.

Inclusion Criteria

We included in the analysis only participants that managed to successfully finish the baseline condition and at least one of the two adaptation conditions. Thus, we excluded participants whose performances were not evaluable (i.e., the psychometric function did not successfully fit) in more than one experimental condition and participants whose Just Noticeable Difference (JND) was negative or higher than the maximum difference in temporal frequency achievable between the test and reference stimuli. We then scan for outliers, excluding participants whose Point of Subjective Equality (PSE) in each experimental condition was ± 2 standard deviations higher or lower than the averaged PSE for that condition within the same age group. After the exclusion process was completed, 28 participants were not included in the final analysis. In the end, we included a total of 91 participants in the final analysis. The distributions of participants included in the

Table 1

Summary Showing Number of Participants in Each Age Group, Together With Gender Distribution, the Mean and Standard Deviation of Age

Age group	n	F	*M* age	Standard deviation
Six	14 (23)	4 (7)	6.561 (6.558)	0.261 (0.268)
Seven	24 (35)	10 (18)	7.469 (7.431)	0.271 (0.272)
Eight	14 (18)	5 (8)	8.354 (8.332)	0.191 (0.184)
Nine	10 (10)	3 (3)	9.386 (9.386)	0.268 (0.268)
Ten	16 (19)	10 (10)	10.435 (10.463)	0.417 (0.443)
Adults	13 (14)	7 (8)	27.429 (27.923)	9.672 (9.886)
High adaptation				
Six	9	3	6.587	0.301
Seven	18	8	7.469	0.281
Eight	13	5	8.4	0.173
Nine	9	3	9.347	0.25
Ten	15	9	10.474	0.411
Adults	13	7	27.923	9.887
Low adaptation				
Six	13	3	6.602	0.224
Seven	16	6	7.458	0.295
Eight	13	4	8.338	0.201
Nine	9	2	9.387	0.285
Ten	13	10	10.467	0.358
Adults	13	7	27.923	9.887

Note. Within parentheses, we reported the number of initial participants, with their related statistics. Outside parentheses, we reported the number of participants that were included in the final analysis, with their relative statistics. In the lower part, we reported the same indices considering the participants that managed to complete the baseline and at least one of the two adaptation conditions.

final analysis are reported in Table 1. The specific motivation for participants' exclusion has been reported in the online supplemental materials.

Vibrators Specifics

The vibrators used were D-frame solenoids with general dimensions of 30 × 16 × 19 mm. Both vibrators were linked to the computer used to run the experiment via a USB cable. The connection between the vibrators and the pilot computer was powered through a dedicated host. The powered connection generated an electromagnetic field able to move a pin placed within the solenoid's coil up and down. The maximum plunger length of the vibrators was 7 mm.

Experimental Procedure

We decided to employ the tactile modality for our tasks rather than the more classical method concerning vision since, in visual adaptation paradigms, it is required that the gaze be fixed on a specific point for a prolonged period. Given the age of the participants in this study, we thus considered this an issue with the potential to cause interference, as the possible absence of aftereffects could be determined by the inability—especially of younger children—to concentrate on the required point for a sufficient amount of time. Conversely, the use of the tactile modality does not present this limitation, as the stimulation is applied directly to the participant's finger and requires less effort in maintaining the same stimulated area.

To begin the experiment, participants sat in front of a customized wooden chamber with their arms outstretched ahead of them. Both participants' indices were placed on top of comfortable support, from which the pin of two vibrators protruded. The vibrators were 38 cm apart, and the participants were placed equidistant from the devices. The wrists of the children were also reclined on a holder so that they could gently lay their indices in the appropriate position and touch the pins of the vibrators with ease. Participants could not see their hands, as the upper part of the chamber occluded their sight.

Experimental Design

Three distinct experimental conditions were developed: baseline, high-, and low-frequency adaptation (see Figure 1). In each of the conditions, the frequency of the reference stimulus was fixed at 10 Hz, while the frequency of the test was varied through a QUEST algorithm (Watson, 2017; Watson & Pelli, 1983) and ranged from 5 Hz to 20 Hz. The reference stimulus was always delivered at the top of the left index, while the test stimulus was always presented at the top of the right index. Both the reference and the test stimuli lasted 1 second. The two stimuli were sequentially presented, and the order of presentation was randomized across trials. The Inter-Stimulus-Interval (ISI) was 1 second. Participants were tested using a two-alternatives forced-choice (2AFC) paradigm.

In the baseline condition, no vibrotactile stimulation was presented before the testing phase, while in both adaptation conditions, a sustained vibrotactile stimulation, namely the adapter, was delivered prior to the presentation of the test and the reference stimuli. In the high-frequency adaptation condition, the adapter ran at 20 Hz, while in the low-frequency adaptation condition, the adapter ran at 5 Hz. Adaptation lasted 6 seconds and was elicited on the top of the right index, on the same portion of skin in which the test stimulus was then delivered shortly after. There was a 1-second interval between the end of adaptation and the beginning of the stimuli presentation. In all three conditions, participants had to verbally indicate which had the higher temporal frequency (i.e., was faster), following the presentation of both the test and reference stimuli. For clarification purposes, the "high" and "low" adaptation terms refer to the frequency around which perceptual performance is evaluated, that is, the frequency of the reference. Because of this, adapting with any of the magnitudes higher than 10 Hz would classify as "high adaptation," while adapting with any of the magnitudes lower than 10 Hz would classify as "low adaptation."

The adult participants performed, on average, a total of 170 trials (70 in the baseline condition, 50 in each adaptation condition), while the children performed 100 trials (40 in the baseline condition, 30 in each adaptation condition). Data were collected in two separate sessions split over different days, ensuring that a minimum of 24 hr had passed between one adaptation condition and the other. In this way, any potential overlap of adaptation effects was avoided. The order of experimental conditions was randomized across participants, and the whole experiment lasted 1 hr in total.

To better involve younger participants, we created the following game: we told all the children that the wooden chamber in front of them was a hen-house, inside of which there were two chickens. Since these chickens were hungry, they would start to gently peck the hands of the child to ask for food, the chicken that was hungrier pecking faster. The objective of the game was simply to indicate which chicken pecked faster.

Data Analysis

To quantify the ability of participants in discriminating tactile temporal frequency, the proportion of trials where the test was perceived as higher in frequency was plotted against the true, physical test frequency and then fitted with cumulative Gaussian functions. The 50% point of the function defines the PSE, that is, the temporal frequency of the test stimulus perceived as equal to the reference's, and is an indicator of the participant's accuracy. The sensitivity is represented by the JND, that is, the change in magnitude that was needed, regarding the reference, so that the test was successfully identified as the faster stimulus at least 25% of the time. The result of the fit is a sigmoid that ranges from 0 to 1, showing the probability participants indicated the test stimulus as the one with the higher temporal frequency, being this probability expressed as a function of the temporal frequency of the test itself.

To estimate adaptation aftereffects, that is, change of accuracy due to adaptation, we evaluate the Magnitude of Adaptation (MoA) for every participant in each adaptation condition, using the following formula:

$$MoA = \frac{PSEadaptation - PSEbaseline}{PSEbaseline}\%$$

MoA values higher than zero indicate a compression, while values lower than zero indicate an expansion of the perceived temporal frequency. MoA values near zero indicate the absence of adaptation aftereffects, as no change in accuracy between adaptation and

Figure 1
Experimental Design
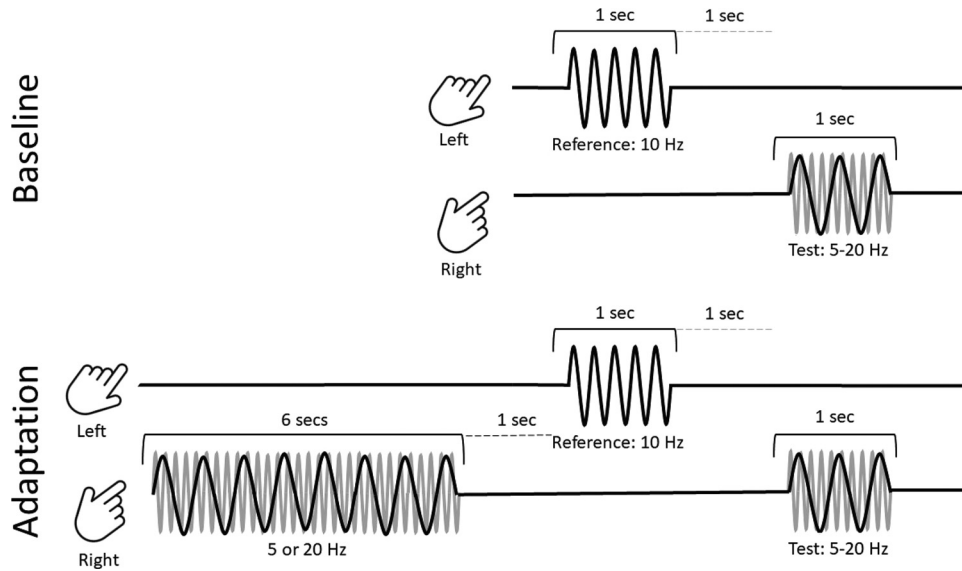
Note. Initially, a baseline condition was run in which a pair of vibrotactile stimulations were sequentially delivered at the top of both participant's indices, in random order (upper panel). Both stimuli were presented for 1 second and were separated by a 1-second interstimulus interval. The stimulus provided at the top of the left index (the reference stimulus) had a fixed frequency of 10 Hz, while the frequency of the stimulus provided at the top of the right index (the test stimulus) varied between 5 (lowest frequency, black line) and 20 Hz (highest frequency, gray line). Participants had to indicate, at the end of each trial, which one of the two stimulations was higher in frequency. Then, two adaptation conditions were implemented (lower panel). Each trial started with a 6-second adaptation phase. Based on the condition, the frequency of the tactile stimulation delivered during the adaptation phase (the adapter) was either 5 Hz (low-frequency adaptation, black line) or 20 Hz (high-frequency adaptation, gray line). Adaptation was always induced at the top of the right index. One second after the adaptation has ended, test and reference stimuli were randomly displayed, and participants had to indicate which one of the two stimulations was higher in frequency.

baseline condition is observed. We included in the final analysis only the participants that managed to successfully finish at least the baseline condition and one of the two adaptation conditions. For each participant, we were able to define at least the MoA in the high-frequency adaptation condition or the MoA in the low-frequency adaptation condition.

Statistical analyses were conducted using the software R (package "lmperm") and JASP (Version 0.14).

Results

Change in Accuracy

To evaluate performance for each participant, we fitted cumulative Gaussian functions into their corresponding individual data (see Figure 2). We thereby obtained an index of PSE and JND for every participant in all three experimental conditions, so that we were able to investigate the effect of adaptation across different stages of life.

To quantify adaptation aftereffects, we evaluated MoA for each age group (Figure 3A). It is clear from Figure 3A that the adaptation effect in both conditions is not present in younger children but begins to be adult-like around the age of 10 years. In fact, MoA for both high-frequency (in dark gray) and low-frequency (in light gray)

adaptations consistently deviate from 0 around age 10. For statistical confirmation, we ran a 2×6 mixed-design ANOVA on MoA with factor condition (high-frequency Adaptation/low-frequency Adaptation) and Age (6/7/8/9/10/adults). To compensate for missing observations, we analyzed the data using random sampling with replacement via bootstrapping (number of repetitions $n = 10,000$). A significant main effect of condition ($F(1, 142) = 18.365$, $p < .001$, $\eta^2 = .09$), and the interaction between the two factors, ($F(5, 142) = 6.083$, $p < .001$, $\eta^2 = .16$) were found, while no significant effect of Age ($F(5, 142) = 1.104$, $p = .38$, $\eta^2 = .03$) was observed. These results confirm that adaptation evoked different aftereffects according to age and that MoA were thus different across the life span.

Posthoc analysis (after Bonferroni correction for multiple comparisons, adjusting the p-value and confidence intervals for comparing a family of 12 estimates) highlighted differences in MoA between conditions (i.e., high-frequency vs low-frequency adaptation) in adults ($t(24) = 4.464$, $p = .001$, 95% CI [9.26, 63.251]) and 10-year-old children ($t(26) = 4.702$, $p < .001$, 95% CI [10.816, 62.976]). Notably, the same difference across conditions was found also when comparing the effect of high-frequency adaptation in adults and low-frequency adaptation in 10-year-old children ($t(24) = 4.897$, $p < .001$, 95% CI [12.776, 66.767]) and, vice versa when comparing the effect of low-frequency adaptation in adults and high-frequency adaptation in 10-year-old children ($t(26) = -4.254$, $p = .003$, 95% CI

Figure 2

Psychometric Curves for Sample Participant in Each Age Group
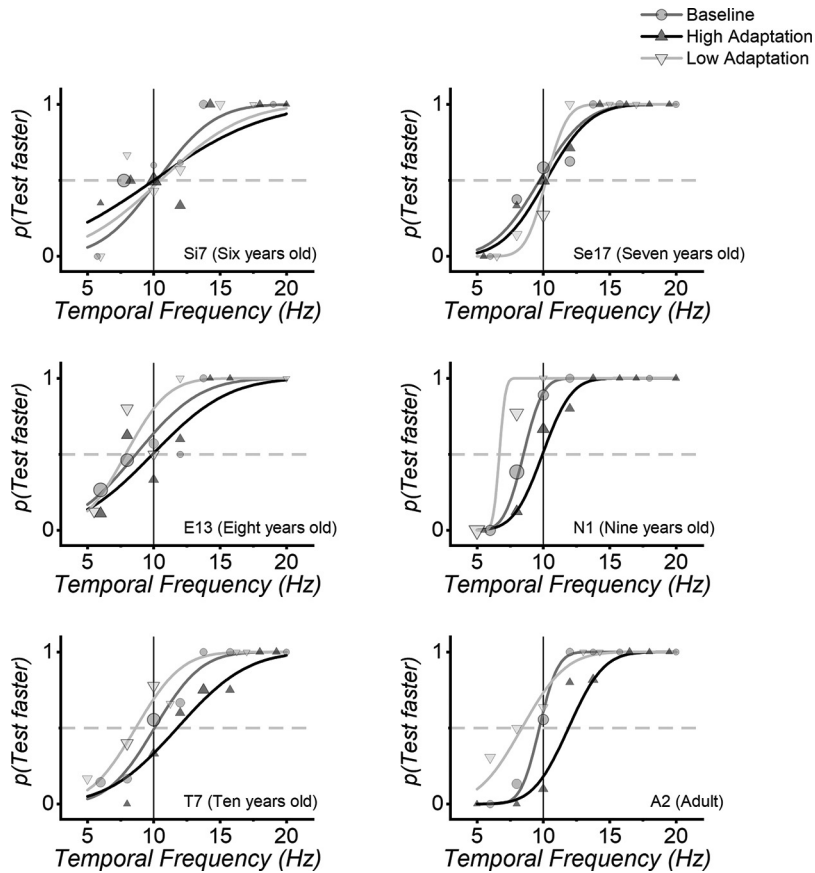
Note. Scatter points represent binned responses (with bins' width set at 2 Hz) for the baseline (dark gray circles), high-adaptation (black triangles) and low-adaptation (light gray upturned triangles) conditions. The size of each symbol is proportional to the number of trials contained within the corresponding bin.

[−59.46, −7.3]). On the other hand, we found no differences between MoA in 6- ($t(20) = −.786$, $p = 1$, 95% CI [−36.902, 22.788]), 7- ($t(32) = −.778$, $p = 1$, 95% CI [−29.152, 18.093]), 8- ($t(24) = 1.087$, $p = 1$, 95% CI [−18.164, 35.827]) or 9- ($t(16) = 2.025$, $p = 1$, 95% CI [−12.682, 52.207]) year-old children, suggesting that both high- and low-frequency adaptation aftereffects consolidate at around 10 years of age.

In addition, to better understand the evolution of adaptation aftereffects during development, we compared MoA against 0 for each adaptation condition within all the age groups. If any effect of adaptation is present at a given age, we should find a significant difference with 0 for the averaged MoA of that age. After correcting for multiple comparisons using Bonferroni's methods (adjusting p-values and confidence intervals for a family of 12 estimates), we confirmed that adaptation did not induce any bias in younger children, as the averaged MoA was not significantly different from 0 in the 6- (high-frequency adaptation: $t(8) = −.232$, $p = 1$, 95% CI [−23.22, 18.98]; low-frequency adaptation: $t(12) = .651$, $p = 1$, 95% CI [−11.58, 21.45]), 7- (high-frequency adaptation: $t(17) = −.212$, $p = 1$, 95% CI [−13.894, 11.359]; low-frequency adaptation: $t(15) = 1.739$, $p = 1$, 95% CI [−.96, 9.483]), 8- (high-frequency adaptation:

$t(12) = 2.743$, $p = .21$, 95% CI [3.537, 30.837]; low-frequency adaptation: $t(12) = 1.278$, $p = 1$, 95% CI [−5.57, 21.595]) and 9- (high-frequency adaptation: $t(8) = 2.254$, $p = .6$, 95% CI [−.414, 36.455]; low-frequency adaptation: $t(8) = −.309$ $p = 1$ 95% CI [−14.734, 11.251]) year-old group. On the other hand, adaptation induced aftereffects in both 10-year-old children (high-frequency adaptation: $t(14) = 3.539$, $p = .036$, 95% CI [9.04, 36.86]; low-frequency adaptation: $t(12) = −4.104$, $p = .012$, 95% CI [−21.354, −6.543]), and adults (high-frequency adaptation: $t(12) = 7.443$, $p < .001$, 95% CI [18.263, 33.382]; low-frequency adaptation: $t(12) = −5.198$, $p = .002$, 95% CI [−14.805, −6.06]).

These results suggest that younger children's judgment is not affected by adaptation to both high and low vibrotactile stimulations. Even though a trend seems to emerge at around 8 years, adult-like behavior consolidates only at 10 years of age. These findings are also confirmed by sample curves obtained fitting psychometric functions into individual participants' data (see Figure 2). When all curves overlap, such as in the 6- and 7-year-old participants, the PSE is not affected by adaptation to either high- or low-frequency vibrotactile stimulations. However, starting from 8 years of age, adaptation begins to shape perception as the curves (and, consequently, the

Figure 3
Performances Across all Age Groups
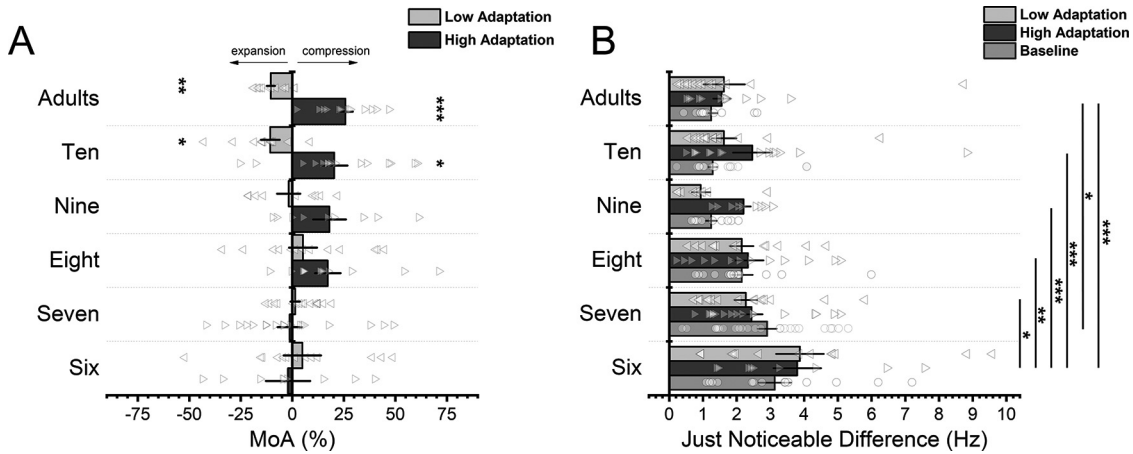
Note. (A) Averaged Magnitude of Adaptation (MoA), grouped per age. As clearly highlighted, vibrotactile adaptation seemed to start biasing perceived temporal frequency at 8 years of age (at least for the high-adaptation condition), even though induced aftereffects become stable only at 10 years of age. Significant comparisons against zero are reported (* $p < .05$; ** $p < .01$; *** $p < .001$). Error bars indicate $\pm$ *SEM*. (B) Just Noticeable Difference across all age groups. Even though sensitivity was lower in the younger groups, adaptation did not cause any change in precision between conditions. Posthoc comparisons for the age factor are reported (* $p < .05$; ** $p < .01$, *** $p < .001$). Error bars indicate $\pm$ *SEM*.

PSE) are progressively shifted away from the baseline. Therefore, high-adaptation starts to induce an underestimation of the test's frequency so that the PSE (the frequency of the test that is perceived as equal to the frequency of the reference) consequentially increases (since now the increased frequency of the test is perceived as fast as the speed of the reference). Conversely, low-adaptation leads to an overestimation of the test's frequency, and the PSE decreases as a consequence.

Change in Precision

To exclude that our results could be explained by a shift in participants' precision due to the presence of the adapter, we investigated the stability of the Just Noticeable Difference (JND) across all experimental conditions (Figure 3B). It is clear from the plot that younger children are less precise than adults in all conditions tested. Thus, we run a 3×6 mixed-design ANOVA on JND with factors condition (baseline/high-frequency adaptation/low-frequency adaptation) and age (6/7/8/9/10/adults). A significant main effect of Age ($F(5, 227) = 9.456$, $p < .001$ $\eta^2 = .163$) was found, while no significant effect of condition ($F(2, 227) = 1.131$, $p = .324$, $\eta^2 = .008$), nor an interaction effect, ($F(10, 227) = .865$, $p = .567$, $\eta^2 = .03$) were present. As one would expect, we found a significant difference among the age groups, in which younger children were less precise than older children and adults (Figure 3B).

Posthoc analysis on age groups (after Bonferroni correction for multiple comparisons, adjusting the p-value and confidence intervals for comparing a family of 6 estimates) highlighted that 6-year-old children were less precise than 7- ($t(36) = -3.296$, $p = .017$, 95% CI [-2.073, $-.142$]), 8- ($t(26) = -3.792$, $p = .003$, 95% CI [-2.408, $-.331$]), 9- ($t(22) = -5.337$, $p < .001$, 95% CI [-3.25, $-.975$]), 10- ($t(28) = -4.963$, $p < .001$, 95% CI [-2.762, $-.736$]) year-old children, and adults ($t(25) = -5.876$, $p < .001$,

95% CI [-3.179, -1.09]). Notably, also 7-year-old children were overall less precise than adults ($t(35) = -3.169$, $p = .026$, 95% CI [-1.959, $-.096$]).

Nonetheless, the groups in which the JND is higher are also the ones in which the aftereffect is lower. Since we found no differences in JND among the three experimental conditions (i.e., no interaction effect between factors), we conclude that adaptation did not impair the sensitivity of the participants in discriminating the temporal frequency of the two vibrotactile stimulations. Thus, any change in performance found in this study must be addressed to accuracy modifications. To investigate whether the absence of adaptation aftereffect was simply masked by the lower precision of younger participants, we evaluated the correlation between sensory precision (i.e., the JND) in the baseline and the module of the MoA across all ages (since here we are interested in the aftereffect's magnitude per se, rather than its direction), both for the high- and the low-frequency adaptation conditions (see Figure 4).

We found that MoA did not correlate with sensory precision in the baseline, with the only exception being the 9-year-old group in the high-adaptation condition ($r(7) = .82$, $p = .006$). Since adaptation aftereffects investigated in our study seem to consolidate at 10 years of age, this correlation might indicate that adaptation aftereffects in the 9-year-old group are, at least partially, influenced by the children's ability to discriminate between the two stimulations (since lesser precise children show the highest effects). This result suggests that observed aftereffects might not be necessarily driven by the presence of the adapter, and those adaptation aftereffects observed in the 9-year-old group might be, at least partially, spurious.

Crucially, we found no other correlation between sensitivity and MoA in other groups, indicating that other adaptation aftereffects highlighted in this study (or their absence) cannot be justified by participants' inability to discriminate the temporal frequency of vibrotactile stimulations.

Figure 4

Correlations Between Sensitivity in the Baseline Condition and MoA Across Age Groups
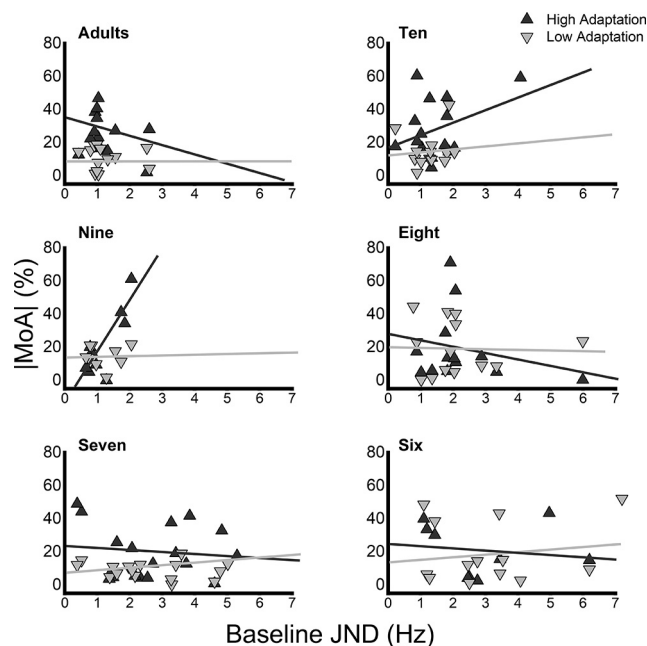
Note. Correlations between sensitivity in the baseline condition (measured as the JND) and MoA in the high-frequency (black triangles and lines) and low-frequency adaptation condition (dark gray triangles and lines). While no correlation between the two parameters was found in most of the age groups, in the 9-year-old group there was a significant positive correlation between the JND in the baseline and the MoA in the high-adaptation conditions.

MoA and Age as a Discrete, Continuous Variable

Since age is a continuous, rather than discrete, variable, to corroborate the hypothesis that vibrotactile aftereffects emerge during development, we computed a Spearman's Rho coefficient to assess the linear relationship between age (expressed on a continuous scale) and MoA (see Figure 5).

We found a positive correlation between high-adaptation aftereffects and age ($\rho_{s(62)} = .392$, $p = .001$) and a negative correlation between low-adaptation aftereffects and age ($\rho_{s(62)} = -.339$, $p = .006$). These results highlight that a monotonic relationship is present between age and MoA and confirm that vibrotactile adaptation aftereffects follow a developmental trend. To better assess when adaptation aftereffects become significant, considering age as a continuous variable, we also fitted regression lines for both high- and low-adaptation induced aftereffects. For high-adaptation induced MoA, the overall regression was statistically significant ($R^2 = .12$, $F(1, 62) = 8.68$, $p = .004$), even though the predictive power of the model was lesser than satisfactory. Similarly, for low-adaptation induced MoA, the overall regression was statistically significant ($R = .11$, $F(1, 62) = 7.77$, p-value $= .007$), but the model was not a good predictor of MoA when expressed as a function of age, mainly due to the noise inherently present in the data.

Nonetheless, both regressions were statistically significant, suggesting once more that a developmental trend determines the evolution of

tactile frequency aftereffects during childhood. Lastly, to pinpoint the age at which adaptation aftereffects emerge, we considered the age point at which the two regression slopes cease to overlap. We found that the two regression slopes stop overlapping at about 8.5 years of age, suggesting that adaptation aftereffects start emerging at that age, even though potentially consolidate only later along with development.

Discussion

The current study aims to unravel how adaptation aftereffects develop along with the life span and whether or not they are inherently present during the early stages of life. To test and validate this, we tracked vibrotactile aftereffects across different ages (from 6 years old to adulthood), using high- and low-frequency adapting stimulations to define the developmental trajectory of vibrotactile frequency adaptation. Our results support the hypothesis that not all sensory adaptation mechanisms are inherently functional in humans and that some of them develop at later stages in life. Our findings can be discussed considering at least a few major points.

First, to the best of our knowledge, the evolution of adaptation aftereffects along typical developmental lines has not previously been investigated before this study. Here, we propose a plausible developmental trajectory of sensory adaptation, a case of well-known psychophysical evidence of specific neural modulations that are still to be fully understood. Our data suggest that sensory adaptation might not be fully developed during the early stages of life and that adult-like perceptual behavior starts to emerge at 8 years of age and is consolidated only at 10 years of age. In fact, our results showed that younger children did not experience adaptation aftereffects after exposure to 6-second vibrotactile adapting stimulations, in opposition to the data gathered from older children and adults.

Second, our study investigated adaptation aftereffects only regarding the tactile modality and solely about temporal frequency perception. Thus, we believe it is crucial to discuss the generalizability of our findings across different sensory channels and perceptual features. Despite our work tracking the development of adaptation aftereffects along with childhood, we note that we were not the first to investigate adaptation aftereffects in children.

Within the visual domain, children experience dark (Dannemiller, 1985; Hansen & Fulton, 1986) and color (Bologna et al., 1984; Suttle et al., 2002) adaptation aftereffects during early infancy, only a few months after birth. However, such aftereffects are modulated by changes at precortical levels (Chang et al., 2016; Dowling & Ripps, 1972) and thus, can be differentiated from cortical adaptation since they do not share similar neural substrates. Nonetheless, there is strong evidence proving that children can experience figural and identity face aftereffects starting from 4 years of age (Jeffery et al., 2010; Short et al., 2011). Although face adaptation is a cortical phenomenon (Webster & Macleod, 2011), both figural and identity face aftereffects cannot be justified by purely low-level adaptation (e.g., tilt adaptation), as they are maintained when adapters of different sizes or orientations are used (Pimperton et al., 2009; Rhodes et al., 2004). Again, this represents a substantial difference with tactile frequency adaptation and can explain why the latter is inefficient in children up to 10 years of age.

Within the tactile domain, it was demonstrated that children experience changes in the amplitude discrimination thresholds when exposed to a preceding vibratory stimulus (Puts et al., 2013, 2014).

Figure 5
Correlations Between MoA and Age
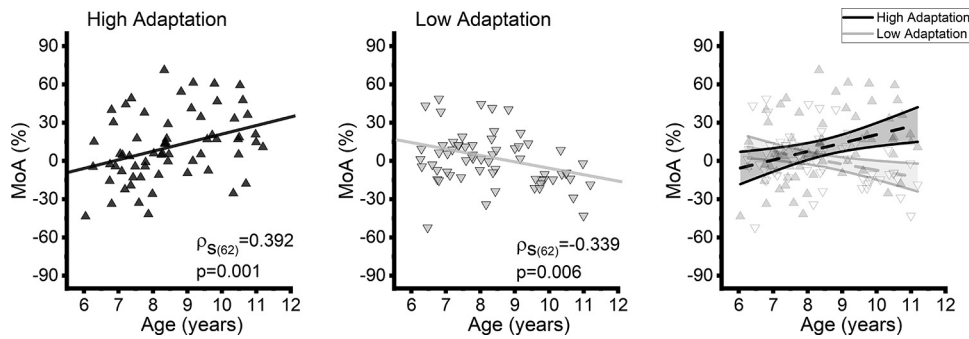
Note. Correlations between MoA observed in the high-adaptation condition and age (left panel, black symbols and line), and between MoA observed in the low-adaptation condition and age (mid panel, gray symbols and line). To assess when adaptation aftereffects arise considering age as a continuous variable, we also fitted regression lines (dashed lines) for both high- and low-adaptation induced aftereffects, evaluating 95% confidence intervals (continuous lines) and considering the age point in which the two slopes do not overlap anymore (right panel).

Still, the intensity perception of tactile stimulations is mediated by local mechanoreceptive channels, the channel with the weakest signal being partially suppressed (Hollins & Roy, 1996). Furthermore, it has been proposed that perceived intensity shifts due to adapting vibratory stimuli may be linked to a local increase in the spiking threshold of receptors' membranes (Bensmaïa et al., 2005). Despite desensitization of mechanoreceptive channels causing an all-around temporary decrement of afferents sensitivity, perceived tactile amplitude and temporal frequency appear to have different physiological substrates (Yau et al., 2009). In the flutter frequency range, while amplitude adaptation has a greater impact on afferents sensitivity than on psychophysical thresholds, frequency adaptation efficacy is uncorrelated with the spectral sensitivity of the afferents, suggesting that adaptation to vibratory frequency is not merely related to the local changes it elicits (Bensmaïa et al., 2005). Even though we did not use vibratory adaptation but rather discrete temporal frequency adaptation, we assume that both types of adaptation-induced modulations can be considered similar. For vibratory stimuli, high-frequency adaptation caused greater threshold shifts than low-frequency adaptation (see (Bensmaïa et al., 2005, Figure 9). Our results in adults are empirically in line with the predicted imbalance of the shift amplitude since the proportionality between the frequency of the adapters and the corresponding magnitude of the aftereffects is not constant (see Figure 2A). We used a 20 Hz and a 5 Hz vibrotactile adapter for the high- and low-frequency adaptation condition, respectively. Thus, the adapter frequency was twice the frequency of the reference in the high-frequency adaptation condition, and half in the low-frequency adaptation condition. Albeit, MoA in the high-frequency condition was more than double the MoA in the low frequency adaptation condition.

Our results, in comparison to previous findings of sensory adaptation in children (Bologna et al., 1984; Dannemiller, 1985; Hansen & Fulton, 1986; Puts et al., 2013, 2014; Suttle et al., 2002), suggest that sensory adaptation suppression might be selectively related to various levels of information processing. Thus, it becomes difficult to assume that sensory adaptation is generally suppressed before certain developmental milestones are reached.

Notably, both high-level cortical adaptation and transducent desensitization appear to be fully functional well before 10 years of age (Bologna et al., 1984; Dannemiller, 1985; Hansen & Fulton, 1986; Puts et al., 2013, 2014; Suttle et al., 2002).

This raises the question, however, as to why vibrotactile adaptation to frequency follows a developmental trajectory. While we do not have clear answers, we can provide speculation considering that, even though vibrotactile adaptation has been found at various levels of information processing (Bensmaïa et al., 2005; O'Mara et al., 1988), only evoked firing rates in S1 covariates with behavioral performance (Salinas et al., 2000). This suggests that if adaptation aftereffects are absent in younger children, cortical activity in S1 after repeated stimulations is unaltered. Interestingly enough, cortical modulation of the neocortex is determined by the activity-dependent depression of thalamocortical synapses, as repeated stimulations seem to reduce the gain of thalamocortical synaptic transmission (Chung et al., 2002). Thus, we can speculate that—during critical developmental periods—thalamocortical synapses are less prone to be distorted by prolonged stimulations and, as a result, cortical signals lead to veridical estimations when performing our task, regardless of the adapter's presence. Furthermore, the thalamic hypothesis seems compatible with previous studies about sensory adaptation in children (Bologna et al., 1984; Dannemiller, 1985; Hansen & Fulton, 1986; Puts et al., 2013, 2014; Suttle et al., 2002) and could explain why afferents desensitization and high cortical adaptation are functional in early childhood, while low-level cortical adaptation is not. Nevertheless, based on the data presented in the current work, we are unable to support anything further than mild speculation, and additional studies are needed to investigate adaptation-induced neural modulations at the cortical and subcortical levels more thoroughly.

On a final note, the covariation between behavioral performance and S1 evoked firing rates also suggests that our data can be safely discussed by excluding a potential cross-hand influence in children, even though evidence of such a mechanism is also lacking in adults (Kuroki et al., 2012). Moreover, the primary somatosensory cortex mainly receives inputs from the contralateral part of the body, and it is hard to physiologically believe that distant skin portions,

afferent to contralateral parts of the body, relate to the same somatosensory receptive field. For this reason, we might safely assume that adapting one hand's finger should not shape tactile perception in the homologous, contralateral finger during development.

In conclusion, we demonstrated that adaptation aftereffects are not, overall, present along with a life span. In our study, neither adaptation to high-frequency vibrotactile stimuli, nor low-frequency adapters, elicited coherent aftereffects in younger children, with adult-like aftereffect emerging at 8 years of age and stabilizing only at 10 years of age. Even though sensory adaptation is not entirely absent during the early stages of life, our findings suggest that the development of adaptation aftereffects is tied to the stage of information processing and, consequently, to the neural substrates involved in them. Furthermore, we speculate that, as short-term depression at the thalamocortical level regulates cortical adaptation, repeated stimulations fail to generate such short-term modulations in young children and—as a consequence—to shape their tactile perception. Nonetheless, we can provide nothing more than speculation about why vibrotactile adaptation is inefficient during the early stages of life. To deeper investigate the hypotheses presented here, future behavioral and neurophysiological studies are undoubtedly needed.

Context of Research

In 1834, while strolling around the falls of Foyers in Scotland, Robert Addams was surprised to note that, after repeatedly looking at the flowing downward flux of water, shifting his gaze toward the surroundings resulted in the illusion that nearby rocks were moving upward. Unwittingly, Addams was the first to describe adaptation aftereffects. After more than 180 years, the neurophysiological mechanisms behind this kind of perceptual distortion have been mostly identified, as they appear to be a consequence of changes at the neuronal response level due to prolonged exposure to a stimulation (Georgeson, 2004). However, it is still unclear the functional role of such misperceptions. We hypothesized that if adaptation aftereffects emerged from the simple tuning of cortical activity, we could expect stronger perceptual distortions in children crossing the critical period when the brain is highly plastic. Surprisingly, our results disproved our initial hypothesis, showing how younger children failed to adapt to repeated tactile stimulations consistently. While we do not have clear explanations for this, we believe that our results might support the involvement of subcortical structures (i.e., the thalamus) in determining developmental changes in how sensory signals in the input are modulated before reaching the cortex. Interestingly, this theoretical conception was tested through computational (Todorov et al., 1997) and animal models (Chung et al., 2002), but never in humans. Therefore, our long-term goal is to evaluate whether, along with development, signal modulation is lacking in other sensory modalities as well, aiming at unraveling how coherent environment representations are built during growth.

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