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## Reciprocal Interactions Between Audition and Touch in Flutter Frequency Perception

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### Abstract

In both audition and touch, sensory cues comprising repeating events are perceived either as a continuous signal or as a stream of temporally discrete events (flutter), depending on the events' repetition rate. At high repetition rates (>100 Hz), auditory and tactile cues interact reciprocally in pitch processing. The frequency of a cue experienced in one modality systematically biases the perceived frequency of a cue experienced in the other modality. Here, we tested whether audition and touch also interact in the processing of low-frequency stimulation. We also tested whether multisensory interactions occurred if the stimulation in one modality comprised click trains and the stimulation in the other modality comprised amplitude-modulated signals. We found that auditory cues bias touch and tactile cues bias audition on a flutter discrimination task. Even though participants were instructed to attend to a single sensory modality and ignore the other cue, the flutter rate in the attended modality is perceived to be similar to that of the distractor modality. Moreover, we observed similar interaction patterns regardless of stimulus type and whether the same stimulus types were experienced by both senses. Combined with earlier studies, our results suggest that the nervous system extracts and combines temporal rate information from multisensory environmental signals, regardless of stimulus type, in both the low- and high temporal frequency domains. This function likely reflects the importance of temporal frequency as a fundamental feature of our multisensory experience.

### Keywords

Multisensory; cross-modal; audio-tactile; somatosensory; flutter

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#### Author Contributions

S.C. and J.M.Y. designed the study and wrote the manuscript. S.C. and K.W.C. performed the experiments and analyzed the data. All authors contributed to the final revisions of the manuscript.

#### Competing Interests

The authors declare no competing interests.

#### Data Availability

Behavioral data (.mat files) are available at [https://github.com/YauLab/AT\\_Flutter](https://github.com/YauLab/AT_Flutter).

## 1. Introduction

Environmental oscillations signal information about objects in our surroundings and our interactions with those objects. Although the oscillations we encounter by audition and touch span a wide range of temporal frequencies, the perception of sensory cues comprising repeating events in both sensory modalities can be organized into two domains depending on the repetition rate of the events. At low repetition rates, signals are perceived as a stream of temporally discrete events. At higher repetition rates (>50 Hz), signals are perceived as a single continuous signal. These two domains are categorized as flutter and vibration in touch, and processing in these domains is mediated by distinct neural populations in the peripheral and central somatosensory systems (Mountcastle *et al.*, 1969; Talbot *et al.*, 1968). Auditory perception can be similarly categorized into these two domains, with acoustic flutter perceived at rates near or below the lower limit for perceiving pitch (Besser, 1967; Krumbholz *et al.*, 2000). Acoustic flutter and pitch also appear to have distinct neural representations (Bendor and Wang, 2007). Given the correspondences between auditory and tactile processing of environmental oscillations, the nervous system likely evolved analogous mechanisms for representing temporal frequency information. A key question in perceptual neuroscience has been whether and how information processing is linked across these sensory modalities.

Audition and touch clearly interact in the perception of high-frequency stimulation (Occelli *et al.*, 2011). Auditory signals influence the detection of faint tactile stimulation (Ro *et al.*, 2009; Wilson *et al.*, 2010). Auditory cues exert attractive biases on the perception of vibration frequency (Yau *et al.*, 2009a) and tactile cues can also bias auditory frequency perception (Yau *et al.*, 2010). These bidirectional interactions in frequency perception may reflect the processing of multimodal neural circuits that represent frequency information signaled by both senses, as suggested by crossmodal adaptation and modeling results (Crommett *et al.*, 2017). Indeed, a number of brain regions respond to both auditory and tactile stimulation (Fuxe *et al.*, 2002; Kayser *et al.*, 2005; Nordmark *et al.*, 2012; Perez-Bellido *et al.*, 2017; Schurmann *et al.*, 2006) and causal manipulation of some regions modulates both auditory and tactile perception (Bolognini *et al.*, 2011; Convento *et al.*, 2018; Yau *et al.*, 2014, 2015). Thus, shared or interactive neural systems likely support the integration of auditory and tactile signals occupying the high-frequency domain.

Much less is known about perceptual interactions between audition and touch in the flutter domain (Badde *et al.*, 2016), despite the fact that analogous neural coding schemes are used to represent auditory and tactile flutter (Bendor and Wang, 2007; Saal *et al.*, 2016) and some cortical neurons have been shown to explicitly signal flutter frequency in both modalities (Lemus *et al.*, 2010; Vergara *et al.*, 2016). We addressed this knowledge gap by testing the influences of auditory signals on tactile flutter perception and of tactile signals on auditory flutter perception. Given the tendency for the nervous system to combine multisensory information that is redundantly signaled and the systematic interactions between auditory and tactile processing of high-frequency stimuli, we predicted that these senses would also reciprocally interact in the processing of flutter signals by exhibiting attractive biases in rate perception. Because flutter rate can be determined for click trains and amplitude-modulated (AM) signals, we also tested whether interactions between audition and touch depended on

the exact composition of the flutter stimulus and whether the auditory and tactile flutter signals must be of matching stimulus types (i.e., both click trains or AM signals) in order for the two senses to interact. We reasoned that establishing the dependence of audio-tactile flutter interactions on stimulus type would provide insights into what neural populations contribute to multisensory interactions in flutter perception, given that click trains and AM stimuli may be represented by distinct neural populations (Eggermont, 1993; Liang *et al.*, 2002; Schreiner and Urbas, 1988). These questions serve as first steps in addressing whether interactions between audition and touch in the temporal frequency domain — a fundamental perceptual dimension — follow principles that generalize from higher-frequency sounds and vibrations to lower-frequency flutter signals.

## 2. Material and Methods

### 2.1. Participants

A total of 38 subjects were recruited for the study. Thirteen subjects (eight females;  $20.1 \pm 1.32$  years; one left-handed) were recruited for experiment 1. Sixteen subjects (nine females;  $22.9 \pm 6.11$  years; one left-handed) were recruited for experiment 2. Thirteen subjects (ten females, mean age  $\pm$  SD  $22.4 \pm 7.69$  years; one left-handed) were recruited for the experiment characterizing unimodal flutter discrimination (see Supplementary information). One subject participated in experiments 1 and 2. Two subjects participated in both the unimodal experiment and one of the main experiments. No participant reported a neurological or psychiatric history. All participants reported normal tactile and auditory sensibilities. All testing procedures were conducted in compliance with the policies and procedures of and approved by the Baylor College of Medicine Institutional Review Board. All participants gave their written informed consent and were paid for their participation.

### 2.2. Tactile and Auditory Stimulation

Tactile and auditory stimuli tested in all three experiments were digitally generated (sample rate: 44.1 kHz) in Matlab 2011b (MathWorks, Natick, MA, USA) and presented with Psychtoolbox-3 (Kleiner *et al.*, 2007) running on a MacBook Pro (model A1278; OS X 10.9.5, 2.5 GHz Core i5, 4 GB of RAM). Tactile stimuli were analog signals passed through one channel of the auxiliary port to a power amplifier (Krohn-Hite Wideband Power Amplifier, model 7500; Krohn-Hite Corp., Brockton, MA, USA) and delivered to the subject's right index finger through an electromechanical tactor (type C-2; Engineering Acoustics, Inc., Casselberry, FL, USA). The tactor was fastened to the distal phalange on the right index finger using self-adherent cohesive wrap bandages. Subjects maintained their hand in a supinated posture during the test blocks. Auditory stimuli consisted of analog signals from the second channel of the auxiliary port. These signals were amplified (PTA2; Pyle Audio, Inc., Brooklyn, NY, USA) and delivered binaurally *via* noise-cancelling in-ear headphones (ATH-ANC23, Audio-Technica U.S., Inc., Stow, OH, USA). In all experiments, subjects also wore noise-attenuating earmuffs (Peltor H10A Optime 105 Earmuff; 3M, St. Paul, MN, USA) over the in-ear headphones, to attenuate any noise produced by the tactor.

Two types of flutter stimulation were tested during the experiments (Fig. 1). Amplitude-modulated (AM) signals (duration: 1 s) were generated with the function:

$$p(t) = [1 + m * \sin(2\pi f_{\text{mod}}t)] * \sin(2\pi f_c t)$$

where  $t$  is time,  $m$  is the modulation index (set to 1 for a modulation depth of 100%),  $f_c$  is the carrier frequency (200 Hz), and  $f_{\text{mod}}$  is the frequency of the modulation envelope which ranged from 16 to 36 Hz. Click train (CT) signals consisted of 1-s trains of monopolar, rectangular pulses (pulse duration: 3 ms). The number of pulses in each click train ranged from 16 to 36.

### 2.3. General Procedures

Before performing the main experimental task, subjects were trained to perform flutter discrimination separately in the auditory and the tactile modalities. Subjects who could not perform the discrimination task reliably were excluded from the main study. A total of 11 subjects were excluded across the full study (experiment 1: 3, experiment 2: 6, unimodal experiment: 3). Experiments 1 and 2 were split into two separate sessions of approximately 1.5 h each, conducted on different days (mean inter-session interval  $\pm$  SD, experiment 1: 6.5  $\pm$  4.7; experiment 2: 4  $\pm$  3.3 days).

### 2.4. Flutter Discrimination Task

Participants discriminated between two flutter stimuli (inter-stimulus interval: 0.8 s) and reported which stimulus was perceived to be higher in frequency in a two-interval, two-alternative forced-choice paradigm (Fig. 1). On each trial, one interval contained the standard stimulus whose frequency ( $f_s$ ) was always 26 Hz. The other interval contained a comparison stimulus whose frequency ( $f_c$ ) was 16, 20, 24, 28, 32, or 36 Hz. The interval containing the standard stimulus was randomized across trials. To ensure that participants could not perform the frequency discrimination task using stimulus intensity cues, each stimulus was delivered at the same nominal amplitude but with a random jitter ( $\pm 10\%$ ). Subjects maintained their gaze on a central fixation cross on a computer screen and reported their decision by button press using their left hand.

In each experiment, participants were instructed to attend to one modality (targets) while ignoring stimulation in the other (distractors). In experiment 1, the targets were tactile flutter cues. In experiment 2, the targets were auditory flutter cues. During each experiment, distractors co-occurred with the targets on 80% of the trials (Fig. 1). Distractors were either a pair of CT or AM stimuli (equal probability). The temporal frequency (i.e., flutter rate) of the distractor co-occurring with the standard stimulus was either 16 (low frequency distractor) or 36 Hz (high frequency distractor). The frequency of the distractor always matched the frequency of the target in the comparison interval. No distractors were presented in the remaining 20% of the trials and performance on these trials established baselines against which performance achieved with distractors could be compared.

### 2.5. Experiment 1: Tactile Flutter Discrimination With Auditory Distractors

We tested whether auditory CT and AM distractors influenced the perception of tactile CT stimuli. For each subject, each comparison stimulus in each distractor condition (low, high,

baseline) was repeated 40 times for a total of 1200 trials over two sessions. Each session was divided into 10 blocks. Subjects were provided rest intervals between each block.

## 2.6. Experiment 2: Auditory Flutter Discrimination With Tactile Distractors

We tested whether tactile CT and AM distractors influenced the perception of auditory CT stimuli. For each subject, each comparison stimulus in each distractor condition (low, high, baseline) was repeated 40 times for a total of 1200 trials over two sessions. Each session was divided into 10 blocks. Subjects were provided rest intervals between each block.

## 2.7. Unimodal Flutter Discrimination Without Distractors

In a separate group of participants ( $n = 10$ ), we characterized participants' ability to discriminate auditory and tactile flutter stimuli in the absence of any distraction. Each subject was tested in a single session. For each modality, we tested CT and AM stimuli. Each stimulus type (CT<sub>T</sub>, CT<sub>A</sub>, AM<sub>T</sub>, AM<sub>A</sub>) was tested in separate blocks and a total of two blocks were run for each stimulus type. The order of the blocks was pseudo-randomized within the session so that two blocks of the same type were never tested consecutively. Each comparison stimulus was presented 20 times yielding a total of 480 trials. Subjects were allowed a short break between each test block.

## 2.8. Data Analysis

All statistical analyses were performed in Matlab. Normality was tested using Kolmogorov–Smirnov tests.

Each participant's choice probability data were fitted with a Gaussian cumulative distribution function (cdf):

$$p(f_c > f_s) = \frac{1}{2} \left[ 1 + \operatorname{erf} \left( \frac{f_c - \mu}{\sigma\sqrt{2}} \right) \right]$$

where  $p(f_c > f_s)$  is the probability that a given  $f_c$  was judged to be higher in frequency than  $f_s$ ,  $\operatorname{erf}(x)$  is the error function of  $x$ , and  $\mu$  and  $\sigma$  are free parameters that represent the participant's point of subjective equality (PSE) and just-noticeable difference (JND), respectively. The PSE is a measure of the perceptual bias and corresponds to the  $f_c$  perceived as equal in frequency to the  $f_s$ . The JND is a measure of the perceptual threshold corresponding to the frequency change (with respect to the standard frequency) that the participant can detect 84% of the time.

## 2.9. Group-Level Analysis

We used the same statistical approach to analyze the data from experiments 1 and 2. To test whether PSE and JND differed in any condition, we first conducted a one-way repeated-measures ANOVA, with distractor condition (five levels: baseline and four distractor conditions) as within-subjects factor. If this test was significant ( $p < 0.05$ ), we then conducted a two-way rmANOVA with distractor type (two levels: CT, AM) and distractor frequency (two levels: 16 Hz, 36 Hz) as within-subjects factors. To compare distractor effects between experiments 1 and 2, we performed a mixed-design ANOVA with distractor

type (two levels: CT, AM), distractor frequency (two levels: 16 Hz, 36 Hz) as within-subjects factors and experiment (which was a proxy for the test and distractor modality pairings in each experiment; two levels: tactile–auditory, auditory–tactile) as the between-subjects factor.

### 3. Results

#### 3.1. Experiment 1: Effects of Auditory Distractors on Tactile Flutter Discrimination

Participants performed a flutter discrimination task with tactile click trains ( $CT_T$ ) in the absence of auditory distraction or while they heard auditory click trains ( $CT_A$ ) or amplitude-modulated ( $AM_A$ ) flutter signals.  $CT_A$  and  $AM_A$  distractors could be higher or lower in frequency compared to the tactile standard stimulus. While participants reliably performed the tactile discrimination task in the baseline and distractor conditions (mean psychometric function  $r^2 \pm SD$ :  $0.98 \pm 0.01$ ), performance patterns changed systematically with both  $CT_A$  distractors (Fig. 2a) and  $AM_A$  distractors (Fig. 2b). A one-way repeated-measures ANOVA conducted on estimates of the point of subjective equality (PSE) indicated that auditory distractors significantly biased tactile performance [ $F_{(4,36)} = 44.50$ ,  $p = 1.8579e-13$ ,  $\eta_p^2 = 0.83$ ] (Fig. 2c). Although baseline performance was unbiased ( $PSE_{Base}$  s.e.m.:  $26.12 \pm 0.15$  Hz), a two-way rmANOVA conducted on PSE estimates in the distractor conditions (Fig. 2d) revealed that the perception of the 26-Hz tactile standard was biased toward the frequency of the auditory distractors ( $PSE_{CT-Low}$ :  $22.14 \pm 0.52$ ;  $PSE_{CT-High}$ :  $26.64 \pm 0.24$ ;  $PSE_{AM-Low}$ :  $21.94 \pm 0.44$ ;  $PSE_{AM-High}$ :  $28.16 \pm 0.51$ ) [frequency main effect:  $F_{(1,9)} = 182.58$ ,  $p = 2.7847e-07$ ,  $\eta_p^2 = 0.95$ ]. The main effect of distractor type did not achieve significance [ $F_{(1,9)} = 1.00$ ,  $p = 0.34$ ,  $\eta_p^2 = 0.10$ ], but there was a significant frequency  $\times$  type interaction [ $F_{(1,9)} = 11.47$ ,  $p = 0.008$ ,  $\eta_p^2 = 0.56$ ] which suggests that distractor effects on PSE may be more pronounced with  $AM_A$  distractors. To better compare the magnitude of distractor effects, we performed a two-way rmANOVA on the absolute PSE differences between the baseline and distractor conditions. This analysis revealed only a significant main effect of frequency [ $F_{(1,9)} = 39.15$ ,  $p = 0.0001$ ,  $\eta_p^2 = 0.81$ ], but no significant effect of type [ $F_{(1,9)} = 4.76$ ,  $p = 0.06$ ,  $\eta_p^2 = 0.34$ ] nor interaction effects [ $F_{(1,9)} = 0.60$ ,  $p = 0.46$ ,  $\eta_p^2 = 0.06$ ]. These results indicate that  $CT_A$  and  $AM_A$  distractors exerted comparable attractive biasing effects on judgments of tactile click trains in a manner that depended on distractor frequency.

A one-way rmANOVA conducted on estimates of the just-noticeable difference (JND) indicated that auditory distractors significantly impaired tactile sensitivity to flutter frequency differences [ $F_{(4,36)} = 4.37$ ,  $p = 0.005$ ,  $\eta_p^2 = 0.33$ ] (Fig. 2e, f). Indeed, relative to baseline discrimination thresholds ( $JND_{Base}$ :  $1.64 \pm 0.16$  Hz), thresholds were higher in the presence of all auditory distractors ( $JND_{CT-Low}$ :  $2.52 \pm 0.51$ ;  $JND_{CT-High}$ :  $2.85 \pm 0.38$ ;  $JND_{AM-Low}$ :  $2.26 \pm 0.31$ ;  $JND_{AM-High}$ :  $2.89 \pm 0.34$ ). To test whether auditory distractor effects on JND depended on distractor conditions, we conducted a two-way rmANOVA which revealed no significant main effects nor interactions [frequency main effect:  $F_{(1,9)} = 3.49$ ,  $p = 0.09$ ,  $\eta_p^2 = 0.28$ ; type main effect:  $F_{(1,9)} = 0.23$ ,  $p = 0.64$ ,  $\eta_p^2 = 0.03$ ; interaction

effect:  $F_{(1,9)} = 0.26$ ,  $p = 0.62$ ,  $\eta_p^2 = 0.03$ ]. These results indicate that auditory distractors impaired tactile sensitivity to flutter frequency in a non-specific manner.

### 3.2. Experiment 2: Effects of Tactile Distractors on Auditory Flutter Discrimination

A separate group of participants performed a flutter discrimination task with auditory click trains (CT<sub>A</sub>) in the absence of tactile distraction or while they felt tactile click trains (CT<sub>T</sub>) or amplitude-modulated (AM<sub>T</sub>) flutter signals. While participants reliably performed the tactile discrimination task in the baseline and distractor conditions (mean psychometric function  $r^2 \pm SD$ :  $0.99 \pm 0.01$ ), performance patterns changed systematically with both CT<sub>T</sub> distractors (Fig. 3a) and AM<sub>T</sub> distractors (Fig. 3b). A one-way rmANOVA conducted on PSE estimates indicated that tactile distractors significantly biased auditory performance [ $F_{(4,36)} = 7.71$ ,  $p = 0.0001$ ,  $\eta_p^2 = 0.46$ ] (Fig. 3c), causing the auditory flutter rate (PSE<sub>Base</sub>:  $25.29 \pm 0.33$ ) to be perceived as more similar to the tactile distractors (PSE<sub>CT-Low</sub>:  $25 \pm 0.17$ ; PSE<sub>CT-High</sub>:  $26.30 \pm 0.23$ ; PSE<sub>AM-Low</sub>:  $24.75 \pm 0.3$ ; PSE<sub>AM-High</sub>:  $26.01 \pm 0.25$ ). A two-way rmANOVA conducted on PSE estimates revealed a significant main effect of distractor frequency [ $F_{(1,9)} = 14.43$ ,  $p = 0.004$ ,  $\eta_p^2 = 0.62$ ], but the main effect of distractor type and the frequency  $\times$  type interaction failed to achieve significance [type main effect:  $F_{(1,9)} = 1.78$ ,  $p = 0.21$ ,  $\eta_p^2 = 0.16$ ; interaction effect:  $F_{(1,9)} = 0.03$ ,  $p = 0.87$ ,  $\eta_p^2 = 0.003$ ]. While the main effect of frequency can be appreciated in the attractive influences of the 16- and 36-Hz tactile distractors on the perceived frequency of the 26-Hz auditory flutter stimulus (Fig. 3c, d), this result does not indicate whether the magnitude of the bias effects differed according to distractor frequency. A two-way rmANOVA conducted on the absolute PSE differences between the baseline and distractor conditions yielded no significant main nor interaction effects [frequency main effect:  $F_{(1,9)} = 0.03$ ,  $p = 0.86$ ,  $\eta_p^2 = 0.004$ ; type main effect:  $F_{(1,9)} = 0.29$ ,  $p = 0.60$ ,  $\eta_p^2 = 0.03$ ; interaction effect:  $F_{(1,9)} = 3.50$ ,  $p = 0.09$ ,  $\eta_p^2 = 0.28$ ]. These results indicate that CT<sub>T</sub> and AM<sub>T</sub> distractors exerted similar attractive biasing effects on judgments of auditory click trains in a manner that depended on distractor frequency.

A one-way rmANOVA conducted on JND estimates (Fig. 3e, f) indicated tactile distractors did not significantly modulate auditory sensitivity to flutter frequency differences [ $F_{(4,36)} = 1.74$ ,  $p = 0.16$ ,  $\eta_p^2 = 0.16$ ] (JND<sub>Base</sub>:  $1.98 \pm 1.98 \pm 0.4$ ; JND<sub>CT-Low</sub>:  $1.92 \pm 0.33$ ; JND<sub>CT-High</sub>:  $1.77 \pm 0.28$ ; JND<sub>AM-Low</sub>:  $2.09 \pm 0.31$ ; JND<sub>AM-High</sub>:  $2.13 \pm 0.36$ ].

### 3.3. Comparison Between Experiments 1 and 2

Flutter discrimination performance by touch and audition was biased by attractive influences of distractors presented in the other modality. To compare the biasing effects in experiment 1 (auditory distractors on tactile flutter discrimination) and experiment 2 (tactile distractors on auditory flutter discrimination), we performed a mixed-design ANOVA on the PSE estimates with distractor type (two levels: CT, AM), distractor frequency (two levels: 16 Hz, 36 Hz) as within-subjects factors and experiment (which was a proxy for the test and distractor modality pairings in each experiment; two levels: tactile–auditory, auditory–tactile) as the between-subjects factor. This analysis revealed significant main effects of experiment [ $F_{(1,18)} = 14.2$ ,  $p = 0.001$ ] and distractor frequency [ $F_{(1,18)} = 162.6$ ,  $p = 1.88e-10$ ], but no

main effect of distractor type [ $F_{(1,18)} = 0.32, p = 0.58$ ]. These results indicate that, while there were no obvious differences between CT and AM distractors, the frequency-dependent distraction effects varied according to the tested modality. This is likely due to the fact that lower-frequency auditory distractors tended to have larger effects while higher-frequency tactile distractors tended to have larger effects. Consistent with this, the experiment  $\times$  type interaction failed to achieve significance [ $F_{(1,36)} = 1.81, p = 0.20$ ], but the remaining interactions were all significant [experiment  $\times$  frequency interaction:  $F_{(1,18)} = 61.3, p = 3.22e-07$ ; type  $\times$  frequency interaction:  $F_{(1,18)} = 7.67, p = 0.013$ ; experiment  $\times$  type  $\times$  frequency interaction:  $F_{(1,18)} = 8.67, p = 0.008$ ]. These interaction patterns reflect strong experiment-specific distractor-frequency effects and more subtle effects of distractor type.

#### 4. Discussion

We rely on multiple sensory modalities to perceive sequences of repeating sensory events in our environment. In auditory and tactile temporal processing, sensory cues comprising events occurring with low repetition rates are perceived as flutter while those occurring with high repetition rates are perceived as a continuous signal associated with a pitch percept. We found that audition and touch interact reciprocally in the perception of flutter cues.

Distractors presented in one modality bias the perception of flutter frequency in the other: A 16-Hz distractor causes a 26-Hz standard stimulus to be experienced as lower in frequency while a 36-Hz distractor causes the same standard stimulus to be experienced as higher in frequency. We also found that flutter information conveyed through click trains and amplitude-modulated distractors induced generally similar biasing effects. These results reveal that the bi-directional interactions between audition and touch in temporal frequency perception, which have been extensively characterized at higher frequencies (>100 Hz), extend down to the flutter frequency domain.

While auditory and tactile signals mutually influence each other in flutter perception, the interaction patterns associated with each distractor modality are marked by subtle differences. We found that the absolute magnitude of auditory biasing effects on tactile perception tended to be greater than the absolute magnitude of tactile biasing effects on auditory perception. This difference may have been attributable to differences in the sensitivity of auditory and tactile flutter perception, assuming that the auditory and tactile flutter cues are combined in a statistically optimal manner (Ernst and Banks, 2002). We tested this indirectly by estimating auditory and tactile flutter discrimination thresholds to CT and AM signals in a separate experiment conducted with a different sample of participants (Fig. 4). The range of thresholds tended to be similar (CT<sub>T</sub>:  $1.58 \pm 0.24$  Hz, CT<sub>A</sub>:  $1.71 \pm 0.38$  Hz, AM<sub>T</sub>:  $3.75 \pm 0.50$  Hz, AM<sub>A</sub>:  $2.12 \pm 0.32$  Hz) and the CT thresholds were statistically indistinguishable from the baseline thresholds in experiments 1 and 2 [CT<sub>T</sub>:  $t(18) = -0.17, p = 0.86$ ; CT<sub>A</sub>:  $t(18) = 0.87, p = 0.40$ ]. Though subtle, the differences in the unimodal thresholds were significantly related to modality [modality main effect:  $F_{(1,9)} = 14.38, p = 0.004, \eta_p^2 = 0.62$ ] and flutter type [main effect:  $F_{(1,9)} = 12.03, p = 0.007, \eta_p^2 = 0.57$ ; interaction effect:  $F_{(1,9)} = 14.06, p = 0.005, \eta_p^2 = 0.61$ ]. Based on these thresholds, if the flutter interactions were simply related to sensitivity differences, we would have predicted larger effects with CT distractors compared to AM distractors; however, we did

not observe larger effects with CT distractors in either experiment. Additionally, given that thresholds were nominally lower for CT<sub>T</sub> stimuli compared to CT<sub>A</sub> stimuli in all experiments without distractors, we would have predicted larger CT distractor effects in Experiment 2 compared to Experiment 1, but this was not observed. Furthermore, threshold patterns with audio-tactile flutter signals were also inconsistent with optimal integration. A maximum likelihood estimation model would predict that the thresholds with the combined sensory cues would be lower than those estimated for each cue separately, but we found that thresholds remained unchanged (with tactile distractors) or were elevated (with auditory distractors). It is possible that the elevated thresholds could reflect the use of a cue-switching strategy where the participants responded according to the auditory distractor rather than the tactile target; however, even if this were the case, it is unclear why such a strategy only applied in Experiment 1. Regardless, the collective interaction patterns imply that auditory and tactile flutter signals were not combined in a statistically optimal manner in our experiments. Our explicit instructions for participants to attend selectively to one modality while ignoring the other may explain this deviation from optimality. Under this context, the goal of the nervous system may not be cue integration, so our paradigm may actually be probing the nervous system's capacity to segregate multisensory cues. Accordingly, auditory distractors may have induced larger biases and elevated thresholds more than tactile distractors in our experiments because it may simply be more difficult to ignore sounds compared to vibration cues in this context. Note, however, that there have been previous reports of optimal statistical inference with low-rate multisensory signals, even when attention is directed toward one modality and away from non-informative signals in another modality (Bresciani *et al.*, 2005; Bresciani and Ernst, 2007; Roach *et al.*, 2006; Wozny *et al.*, 2008). Why the results of these studies differ from ours is unclear at this time, but these collective findings contribute to the growing appreciation that one cannot assume multisensory cue integration; cues may combined or separated depending on the context and task demands (Roach *et al.*, 2006; Shams and Beierholm, 2010; Wozny *et al.*, 2008).

Auditory and tactile distractors also appeared to differ in the relative magnitudes of the PSE shifts induced by the low- and high-frequency distractors. With auditory distractors, low-frequency signals induced significantly larger biases than high-frequency signals. With tactile distractors, high-frequency signals tended to induce larger biases than low-frequency signals, though this difference was not statistically significant. These asymmetries are beyond the scope of the current study, but it is notable that lower-frequency sounds also exert greater influences on vibrations compared to higher-frequency sounds for signals exceeding 100 Hz (Yau *et al.*, 2009a). Based on interaction patterns in high-frequency processing, we previously speculated that this asymmetry could reflect the tuning properties of cortical neurons which may be patterned on the statistics of our sensory experiences (Yau *et al.*, 2009a) and our current results extend this logic to processing in the flutter domain. Indeed, the final estimate computed from the integration of any pair of auditory and tactile signals in a Bayesian framework (Ma and Pouget, 2008) would also depend on the prior reflecting the history of co-occurring audio-tactile signals; if tactile signals tend to be slightly lower in frequency than co-occurring auditory signals in our lifetime of experiences, such a prior could explain the asymmetric PSE patterns in both of our experiments. In the

future, it will be important to measure the actual statistics of our audio–tactile experiences to test Bayesian accounts of audio–tactile integration explicitly.

We investigated whether audio–tactile interactions in flutter processing differ when click trains and amplitude-modulated signals are tested. One possibility was that flutter interactions would only be observed when the auditory and tactile stimulus type matched. Because CT and AM signals may be represented by distinct neural populations (Eggermont, 1993; Liang *et al.*, 2002; Schreiner and Urbas, 1988), interactions mediated by these populations would presumably be sensitive to stimulus type. Furthermore, because CT and AM signals are so perceptually distinct, the interactions between CT and AM signals may have been weaker if flutter interactions depended on the inference of a common cause under a causal inference framework (Shams and Beierholm, 2010). The other possibility was that auditory and tactile flutter interactions occur irrespective of stimulus type. This result would imply that auditory and tactile flutter processing converges on neural populations that support flutter representations which are invariant to stimulus type. We found little evidence that flutter information is combined over the senses in manners that strongly depend on stimulus type. This result could also imply that audio–tactile interactions in flutter processing occur at decisional levels where the flutter information has already been extracted from each stimulus and modality.

What neural populations mediate interactions between auditory and tactile flutter? There have been extensive studies on the neural coding of tactile flutter (Mountcastle *et al.*, 1969, 1990; Romo and Salinas, 2003) and auditory flutter (Bendor and Wang, 2007; Lemus *et al.*, 2009a, b) that have mapped perceptual decision making processes to the sensory and frontal cortices. Recent studies have identified neural populations in traditionally-defined sensory cortices that respond to flutter signals experienced in both modalities (Lemus *et al.*, 2010); however, the weak relationship between perception and the crossmodal activity in these areas implies that multimodal encoding and perceptual judgments are supported by neurons residing in regions outside of the sensory cortices (Lemus *et al.*, 2010). These population may instead be found in frontal regions like pre-supplementary motor area (Vergara *et al.*, 2016) and medial premotor cortex (Haegens *et al.*, 2017) where individual neurons represent auditory and tactile flutter analogously. While neurons in frontal regions have been shown to support unimodal comparisons between pairs of tactile signals or auditory signals and crossmodal comparisons between tactile and auditory signals, the role of these neurons in representing combinations of co-occurring auditory and tactile signals remains to be tested. It will also be critical to determine whether the neural populations which represent auditory and tactile flutter also encode visual flicker (Gebhard and Mowbray, 1959), particularly because auditory flutter and visual flicker interact strongly in rate perception (Badde *et al.*, 2016; Levitan *et al.*, 2015; Lunghi *et al.*, 2014; Recanzone, 2003; Shipley, 1964; Welch *et al.*, 1986).

Audition and touch are known to interact reciprocally in the processing of signals comprising frequencies greater than 100 Hz (Crommett *et al.*, 2017; Ro *et al.*, 2009; Wilson *et al.*, 2010; Yau *et al.*, 2009a, 2010). The nervous system may exploit multisensory information in this frequency domain to support texture perception (Jousmäki and Hari, 1998; Manfredi *et al.*, 2014; Yau *et al.*, 2009b) and sensorimotor processing of fundamental

frequencies in speech (Lattner *et al.*, 2005). Here, we extended the frequency range over which audition and touch interact to the flutter domain. These findings provide yet another example of how the nervous system combines analogous information across sensory modalities. Our psychophysical results can motivate future neurophysiological studies aimed at identifying the neural substrates which underlie multisensory flutter interactions. Moreover, given the importance of slow temporal variations in the speech processing (Drullman *et al.*, 1994) and other behaviors, our findings highlight new ways in which multisensory processes may be leveraged in neurorehabilitation or sensory substitution approaches.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

## Acknowledgements

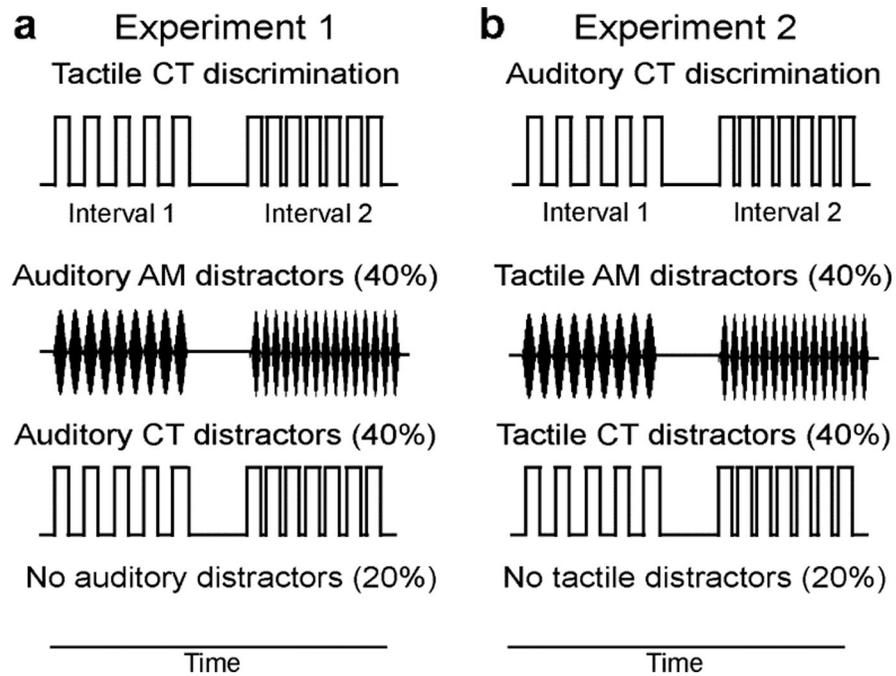
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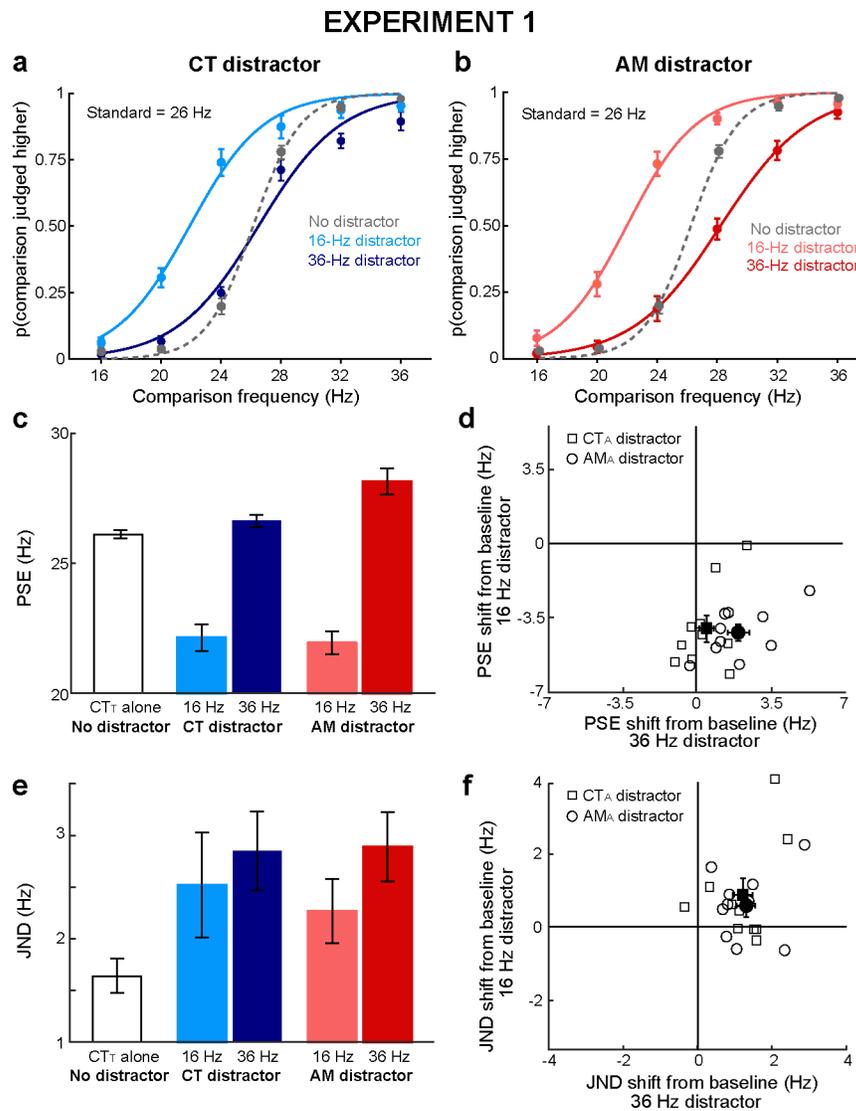
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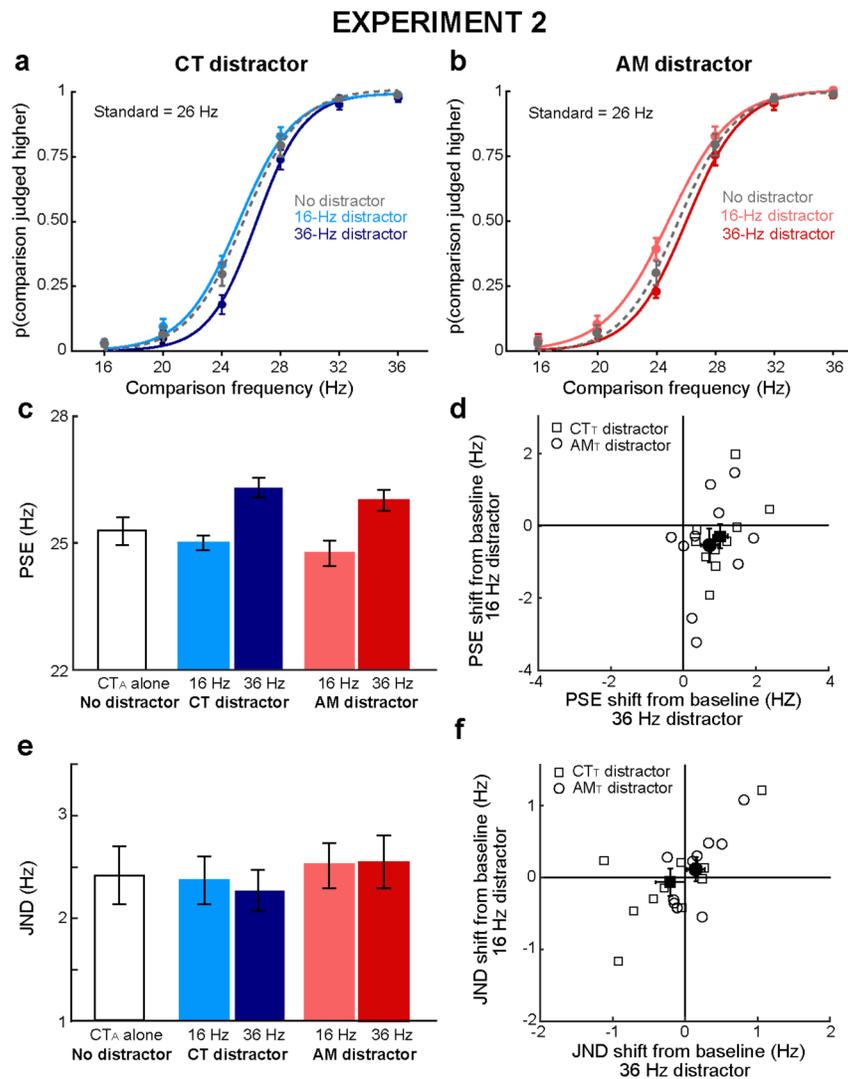
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**Figure 1.**

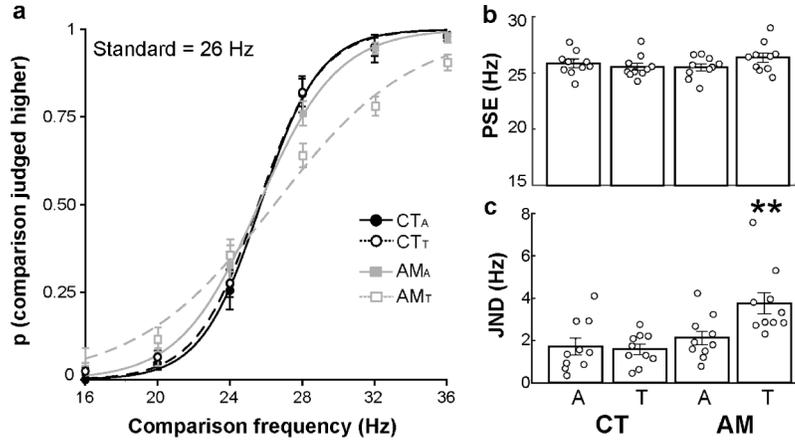
Experimental design; (a) Paradigm used in Experiment 1. Participants performed a two-interval, two-alternative forced choice task to judge which tactile click train (CT) stimulus was perceived to be of a higher flutter rate. The tactile stimuli could be paired with auditory amplitude-modulated (AM) signals, CT signals, or no sounds. (b) Paradigm used in Experiment 2. Participants performed a two-interval, two-alternative forced choice task to judge which auditory CT stimulus was perceived to be of a higher flutter rate. The auditory stimuli could be paired with tactile AM signals, CT signals, or no touch.



**Figure 2.** Tactile flutter discrimination with and without auditory distractors;  $n = 10$  (a, b) Group averaged choice probability data and psychometric functions in the presence of auditory click train (a) and amplitude-modulated (b) distractors. Lighter traces indicate performance with 16-Hz distractors. Darker traces indicate performance with 36-Hz distractors. Dashed grey lines represent performance in trials without distractors. (c) Average PSE estimates under baseline and distractor conditions. (d) Baseline-corrected PSE estimates with low- and high-frequency distractors. Open markers indicate data for individual subjects. Filled markers indicate group average. (e) Average JND (sensitivity) estimates under baseline and distractor conditions. (f) Baseline-corrected JND estimates with low- and high-frequency distractors. Open markers indicate data for individual subjects. Filled markers indicate group average. Error bars indicate s.e.m.



**Figure 3.** Auditory flutter discrimination with and without tactile distractors;  $n = 10$  (a, b) Group averaged choice probability data and psychometric functions in the presence of tactile click train (a) and amplitude-modulated (b) distractors. Lighter traces indicate performance with 16-Hz distractors. Darker traces indicate performance with 36-Hz distractors. Dashed grey lines represent performance in trials without distractors. (c) Average PSE estimates under baseline and distractor conditions. (d) Baseline-corrected PSE estimates with low- and high-frequency distractors. Open markers indicate data for individual subjects. Filled markers indicate group average. (e) Average JND (sensitivity) estimates under baseline and distractor conditions. (f) Baseline-corrected JND estimates with low- and high-frequency distractors. Open markers indicate data for individual subjects. Filled markers indicate group average. Error bars indicate s.e.m.



**Figure 4.** Auditory and tactile flutter discrimination without distractors;  $n = 10$ . (a) Group averaged choice probability data and psychometric functions for auditory click trains (filled circles, solid black line), tactile click trains (unfilled circles, dashed black line), auditory amplitude-modulated stimuli (filled squares, solid grey line), and tactile amplitude-modulated stimuli (unfilled squares, dashed grey line). (b) Average PSE estimates with each stimulus type. Markers indicate data from individual subjects. (c) Average JND estimates with each stimulus type. Conventions as in (b). Error bars indicate s.e.m.