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RESEARCH ARTICLE

Sound enhances touch perception

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Abstract Certain sounds, such as fingernails screeching down a chalkboard, have a strong association with somatosensory percepts. In order to assess the influences of audition on somatosensory perception, three experiments measured how task-irrelevant auditory stimuli alter detection rates for near-threshold somatosensory stimuli. In Experiment 1, we showed that a simultaneous auditory stimulus increases sensitivity, but not response biases, to the detection of an electrical cutaneous stimulus delivered to the hand. Experiment 2 demonstrated that this enhancement of somatosensory perception is spatially specific—only monaural sounds on the same side increased detection. Experiment 3 revealed that the effects of audition on touch are also frequency dependent—only sounds with the same frequency as the vibrotactile frequency enhanced tactile detection. These results indicate that auditory information influences touch perception in highly systematic ways and suggest that similar coding mechanisms may underlie the processing of information from these different sensory modalities.

Keywords Multisensory · Audition · Touch · Perception · Human · Psychophysics

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Introduction

Our perceptual systems are frequently confronted with simultaneous information from multiple sensory modalities. For example, while hearing the buzzing sound of a mosquito, we may also feel the mosquito attempting to land on our neck. Although there have been numerous studies of auditory-visual (Bertelson and Aschersleben 1998; Recanzone 1998; Bertelson 1999; Vroomen and Gelder 2000) and visual-tactile interactions (Rock and Victor 1964; Rock et al. 1965; Tipper et al. 1998, 2001; Ernst et al. 2000; Pavani et al. 2000; Kennett et al. 2001; Ro et al. 2004), little is known about the psychological rules governing the interactions between sound and touch.

This is not because the two modalities are unrelated. Indeed, some studies have shown that certain types of sounds can affect some aspects of touch perception in systematic ways (Gescheider et al. 1969; Sherrick 1976; Jousmaki and Hari 1998; Guest et al. 2002; Hotting and Roder 2004; Navarra et al. 2007; Serino et al. 2007) and that touch can also affect sound perception (Gillmeister and Eimer 2007). In fact, under some conditions, sound alone can invoke certain somatosensory percepts, such as the sound of fingernails scratching a chalkboard (Halpern et al. 1986). We may also feel the vibrations from a loud car stereo, experience tingling sensations from a ringing phone, or feel sharpness from the sound of breaking glass. These strong associations between sound and touch may be a consequence of similar encoding mechanisms: both senses process information that produces mechanical displacements of tissue (i.e., the tympanic membrane for auditory and the skin for somatosensory) and are processed in frequency-based codes in adjacent regions of the cerebral cortex.

In addition to cortical proximity, the somatosensory cortex projects to regions of auditory cortex (Schroeder et al.

2001) and neuroimaging studies have demonstrated interactions between the somatosensory and auditory modalities in some regions of auditory cortex (Foxe et al. 2002). Other studies have also shown direct anatomical connections between auditory and visual cortex at early stages of the cortical processing hierarchy (Falchier et al. 2002; Rockland and Ojima 2003; Clavagnier et al. 2004; Bizley et al. 2007). These demonstrations of interconnectivity between the primary sensory cortices of different sensory modalities have led some to question whether any cortex is truly unisensory (Macaluso and Driver 2005; Schroeder and Foxe 2005; Ghazanfar and Schroeder 2006) and suggest that the perceptual processing of information in one sensory modality may have systematic effects on the processing of information in a different sensory modality.

In order to assess the perceptual interactions between sound and touch, we conducted three psychophysical experiments examining the effects of a task-irrelevant auditory stimulus on the perception of weak somatosensory events. Weak somatosensory stimuli were used because multisensory interactions are known to be most potent for near threshold stimuli (Stein and Meredith 1993). Experiment 1 examined whether a simultaneously presented tone affects somatosensory perception. Experiment 2 examined whether the spatial location of the sound affects somatosensory processing in a spatially specific manner. Experiment 3 examined whether the effects of sound on vibrotactile perception are frequency specific. All three experiments found systematic enhancing effects of sound on somatosensory perception.

Experiment 1

Experiment 1 examined whether an auditory tone affects somatosensory perception. Thus, a centrally perceived, behaviorally-irrelevant sound was simultaneously presented with a near threshold electrical cutaneous stimulus on the critical trials. In the baseline trials, the somatosensory stimulus was delivered without any sound. The detection rates for detecting the somatosensory stimulus with sounds was compared to the detection rates for detecting it alone.

Methods

After informed consent, 20 participants (10 males; 10 females; mean age = 19.05 years) completed this experiment in exchange for course credit. All subjects were neurologically normal and reported no hearing or somatosensory deficits.

The somatosensory stimulus, which was generated using an optically isolated Grass SD9 stimulator, was a 0.3 ms square-wave electrical current that was passed through a pair of ring electrodes attached to the middle finger of the left hand. The participants comfortably rested their left hand on the armrest of a chair below the left speaker. In each subject, the intensity of this electrical cutaneous stimulus, which felt like a faint tap or pulse in the finger, was adjusted to a near-threshold level of 50% detection by varying intensities across blocks of trials until between 4 and 6 stimuli out of 10 were detected. The auditory stimulus, which was a pure 500 Hz sine-wave tone, was delivered via two computer speakers that were approximately 30 cm to the left and right of a centrally located fixation light emitting diode (LED). The tone was 200 ms in duration, 59 dB in intensity, and produced the percept of a central sound.

Participants fixated the central LED, which signaled the start of each trial with a 200 ms flash. Three hundred ms after fixation offset, one of four conditions was delivered: auditory stimulus alone, somatosensory stimulus alone, auditory stimulus with somatosensory stimulus, or no stimuli. Participants performed a two-alternative, forced-choice (2-AFC) task; they verbally reported on each trial whether or not they felt the somatosensory stimulus and were instructed to ignore the auditory stimulus. Once the verbal response of the participant was entered into the computer by the experimenter, the next trial commenced after 500 ms. A total of 160 trials (40 trials for each condition) was completed by each participant.

Results and discussion

An ANOVA was conducted on the behavioral responses, with auditory stimulus (present vs. absent) and somatosensory stimulus (present vs. absent) as the two within-subject factors and the proportion of trials that resulted in a somatosensory percept as the dependent variable. There was a highly significant main effect of the somatosensory stimulus on detection ($F_{1,19} = 96.32$, $P < 0.001$), demonstrating that the electrical current successfully produced a somatosensory percept. The main effect of the auditory stimulus was not significant ($F_{1,19} = 2.25$, $P = 0.15$), indicating that sound alone could not reliably produce a somatosensory percept. However, there was a significant interaction between the auditory stimulus and somatosensory stimulus factors ($F_{1,19} = 6.69$, $P = 0.02$), showing that sound can modulate somatosensory perception. As shown in Fig. 1 and Table 1, this interaction was due to a significant increase in the detection rate for somatosensory stimuli when they were accompanied by an auditory stimulus (61.6% vs. 57.4%; $t_{19} = 2.121$, $P = 0.047$). Importantly, although the sound increased the detection rate when a somatosensory stimulus was presented, the sound did not increase the false alarm rate for reporting a somatosensory stimulus when none was presented (3.4% for sound present vs. 3.4% for sound absent; $F < 1$). This shows that the increase in the detection

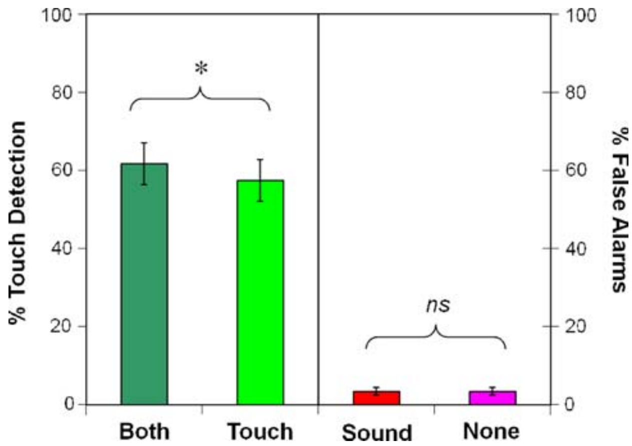

Fig. 1 The data from Experiment 1 examining the effects of audition on touch perception. The *left half* of the figure shows the hit rates, whereas the *right half* of the figure illustrates the false alarm rates. *Error bars* reflect ± 1 standard error of the mean

rate for somatosensory stimuli with sounds was not due to confounding factors, such as feeling mechanical vibrations or air pressure from the speakers.

Signal detection analyses were also conducted to assess the changes in sensitivity independent of or with minimal influences from response biases. For this analysis, d' values for the two auditory stimulus conditions were calculated from the hit (detection report when a somatosensory stimulus is present) and false alarm (detection report with no somatosensory stimulus) rates and subjected to a two-tailed paired t-test. There were significantly higher d' values for detecting the somatosensory stimulus with the sound present ($d' = 2.81$) as compared to the sound absent conditions ($d' = 2.40$; $t_{19} = 2.721$, $P = 0.014$). The c values to measure any potential response biases were also calculated for each auditory stimulus condition. There were no differences in response biases between the sound present ($c = 0.99$) vs. sound absent ($c = 0.97$) conditions ($t_{19} = 0.16$, $P = 0.88$), indicating that the effects of the sound were not a consequence of shifts in response criteria.

These results indicate that a task-irrelevant sound can enhance somatosensory perception. The sounds in this experiment were perceived to come from directly in front of the subject, while the somatosensory stimuli were delivered

Table 1 The mean hit rates for all experiments and the false alarm rates along with the d' and c values for Experiments 1 and 2

	Hits	False alarms	d'	c
Experiment 1				
Sound present	0.62 (0.24)	0.03 (0.09)	2.81 (1.13)	0.99 (0.56)
Sound absent	0.57 (0.24)	0.03 (0.06)	2.40 (0.90)	0.97 (0.53)
Experiment 2				
Touch left-sound left	0.51 (0.21)	0.02 (0.04)[a]	2.38 (0.95)	1.18 (0.30)
Touch left-sound right	0.47 (0.18)	0.04 (0.07)[b]	2.04 (0.94)	1.11 (0.40)
Touch left-no sound	0.46 (0.19)	0.02 (0.05)[c]	2.29 (0.92)	1.26 (0.32)
Touch right-sound left	0.38 (0.18)	0.03 (0.06)[a]	1.93 (0.78)	1.28 (0.42)
Touch right-sound right	0.42 (0.15)	0.03 (0.04)[b]	1.99 (0.68)	1.20 (0.34)
Touch right-no sound	0.37 (0.17)	0.03 (0.05)[c]	1.87 (0.90)	1.33 (0.35)
No touch-sound left	–	0.05 (0.06) 0.04 (0.05)[d]	–	–
No touch-sound right	–	0.03 (0.03) 0.07 (0.10)[d]	–	–
No touch-no sound	–	0.03 (0.04) 0.03 (0.05)[d]	–	–
Experiment 3				
100 Hz Touch-100 Hz sound	0.78 (0.21)	–	–	–
100 Hz Touch-200 Hz sound	0.49 (0.30)	–	–	–
100 Hz Touch-no sound	0.57 (0.31)	–	–	–
200 Hz Touch-100 Hz sound	0.37 (0.17)	–	–	–
200 Hz Touch-200 Hz sound	0.71 (0.19)	–	–	–
200 Hz Touch-no sound	0.67 (0.33)	–	–	–

Only hit rates were measured in the two-alternative forced-choice task of Experiment 3. Standard deviations are in parentheses

[a] This false alarm rate reflects the mean proportion of trials that participants incorrectly reported feeling a sensation on the hand opposite the sound and touch

[b] This false alarm rate reflects the mean proportion of trials that participants incorrectly reported feeling a sensation on the hand opposite the touch, but on the same side as the sound

[c] This false alarm rate reflects the mean proportion of trials that participants incorrectly reported feeling a sensation on the hand opposite the touch

[d] The left false alarm rate reflects the mean proportion of trials that participants incorrectly reported feeling a sensation on the left hand, whereas the right false alarm rate reflects the mean proportion of trials that participants incorrectly reported feeling a sensation on the right hand

to only the left hand. This spatial separation might have limited the increase in somatosensory perception because previous studies in our laboratory have shown that the enhancing effects of vision on somatosensory perception are spatially specific (Johnson et al. 2006). Therefore, Experiment 2 asked whether spatial congruence is important for the effects of audition on somatosensation.

Experiment 2

Experiment 2 examined whether the effects of sound on somatosensory perception are lateralized. Instead of a central sound and a left-hand somatosensory stimulus, as in Experiment 1, the auditory and somatosensory stimuli were delivered to either the left or right of the subject. Thus, the auditory and somatosensory stimuli could be on the same or opposite sides when the sound was presented. Furthermore, Experiment 2 used a set of sound-isolating headphones rather than speakers to lateralize the sounds and to eliminate any potential effects or interactions on somatosensory processing from air pressure. We hypothesized that, compared with the no auditory stimulus condition, a congruent auditory stimulus on the same side as the somatosensory stimulus would improve somatosensory discrimination, while an incongruent sound on the opposite side would result in poorer discrimination.

Methods

After informed consent, 20 participants (8 males; 12 females; mean age = 19.15 years) who did not participate in Experiment 1 completed this experiment in exchange for course credit. All subjects were neurologically normal and reported no hearing or somatosensory deficits.

As in Experiment 1, the somatosensory stimuli were near-threshold electrical stimuli that were delivered through ring electrodes attached to the middle finger of the left and right hands. Each subject comfortably positioned their left and right hands on the arms of their chair. The somatosensory stimulation intensity was first adjusted separately for each hand to a near-threshold level at which 4–6 stimuli out of 10 were felt. The behaviorally-irrelevant auditory stimulus, which was a pure 500 Hz sine-wave tone of 200 ms duration, was delivered to either the left or the right ear via Direct Sound EX-29 Extreme sound-isolating headphones. Because headphones were used, the intensity of the sound (80 dB) was louder than Experiment 1.

This experiment used a three auditory stimulus (none, left, right) ×3 somatosensory stimulus (none, left, right) factorial design for a total of nine conditions. Participants fixated a centrally located light emitting diode (LED), which flashed for 200 ms to signal the start of each trial. Three hundred ms after fixation offset, one of the nine conditions was randomly presented with the constraint that no more than two trials in a row were identical. The participants performed a three-alternative force choice (3-AFC) task, reporting to the experimenter (who entered the response into the computer) whether a left somatosensory stimulus, a right somatosensory stimulus, or no somatosensory stimulus was felt by saying “left,” “right,” or “none”. The next trial began 500 ms after response input.

A total of 360 trials were completed by each subject in this experiment. Collapsed over left and right stimulation sides, this yielded 80 trials for each of the three conditions of main interest: somatosensory stimulus without auditory stimulus, somatosensory stimulus with auditory stimulus on the same side, and somatosensory stimulus with auditory stimulus on the opposite side of space. The remaining trial types (the 120 no somatosensory stimulus trials) were included for signal detection analyses.

Results and discussion

Table 1 provides the data for each of the nine conditions in this experiment. An initial two-way ANOVA was conducted for all of the trials on which a somatosensory stimulus was delivered, with auditory stimulus (left, right, none) and side of somatosensory stimulus (left, right) as the two within subject factors. The main effects of auditory stimulus and side of somatosensory stimulus were not significant (both Ps > 0.10). However, there was a significant interaction between these two factors ($F_{2,38} = 3.27$, $P = 0.049$), which was mainly due to better somatosensory localization rates when the auditory stimulus was on the same side as the sound (i.e., left auditory stimulus with left somatosensory stimulus and right with right) than when they were on opposite sides (i.e., left with right and right with left).

In order to further assess the nature of this interaction, side of stimulation was collapsed in a subsequent one-way ANOVA, resulting in three levels of auditory stimulation with respect to somatosensory stimulation (same side as somatosensory stimulus, opposite side as somatosensory stimulus, none). This additional analysis further confirmed a significant main effect of auditory stimulation on somatosensory localization accuracy ($F_{2,38} = 3.90$, $P = 0.029$). As shown in Fig. 2, when the sound was presented on the same side as the somatosensory stimulus, discrimination rates (46.5%) were significantly greater than when the sound was presented on the opposite side (42.6%; $t_{19} = 2.387$, $P = 0.028$) and when no sound was delivered (41.6%; $t_{19} = 2.691$, $P = 0.014$). The difference in somatosensory discrimination rates between the no sound and the opposite sound conditions was not significant ($t_{19} = 0.495$, $P = 0.626$), indicating that there was no cost associated with sounds delivered to the side opposite to the cutaneous

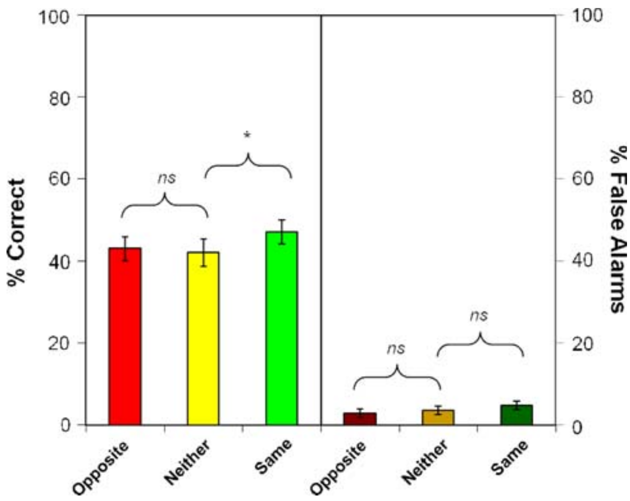

Fig. 2 The data from Experiment 2 examining the spatial specificity of auditory influences on touch perception. The *left half* of the figure shows the hit rates, whereas the *right half* of the figure illustrates the false alarm rates. *Error bars* reflect ± 1 standard error of the mean

stimulus. These results indicate that when an auditory stimulus was delivered to the same side as the somatosensory stimulus, there was a significant enhancement for spatially discriminating the side of the somatosensory stimulus with this simultaneous irrelevant sound.

Since subjects reported on each trial whether they felt something on the left, right, or on neither side, false alarms occurred when participants reported feeling something that was not actually presented (i.e., erroneous reports of a somatosensory percept on one hand when no somatosensory stimulus was delivered or when it was delivered to the opposite hand). The false alarm rates were low for all auditory stimulation conditions (see Table 1). An initial two-way ANOVA on the false alarm rates was conducted, with auditory stimulus (left, right, none) and side of false alarm (left, right) as the two within-subject factors. There was a significant main effect of auditory stimulus that was mainly due to higher false alarm rates for trials with a sound as compared to trials without any sound ($F_{2,38} = 5.45$, $P = 0.009$). The main effect of side of false alarm was not significant ($P > 0.10$). However, the interaction between auditory stimulus and side of false alarm was significant ($F_{2,38} = 5.63$, $P = 0.007$). This interaction was primarily due to subjects making more left-sided false alarms when the auditory stimulus was on the left side and more right-sided false alarms when the auditory stimulus was on the right side.

In order to further assess the nature of this interaction, we averaged the false alarm rates across left and right sides and classified the false alarms as being same-sided when a subject reported feeling something on the same side as the sound when no cutaneous stimulus was provided or reported feeling something on the same side as the sound even though the cutaneous stimulus was delivered to the opposite hand. Similarly, opposite-sided false alarms were computed by averaging across trials on which participants reported feeling a somatosensory stimulus on a hand opposite a sound, regardless of whether a somatosensory stimulus was delivered to the other hand or not. For the no sound trials, the false alarm rates were averaged across the no somatosensory stimulus and the somatosensory stimulus on the opposite hand trials. When a false alarm was made on a trial in which a sound was delivered, participants were more likely to report it on the same side as the sound as compared to the opposite side (4.8% vs. 2.8%; $t_{19} = 2.447$, $P = 0.024$), regardless of whether or not a somatosensory stimulus was delivered to the opposite hand. However, there was only a marginally significant difference between false reports of somatosensation on the same side as the sound and the no sound conditions (4.8% vs. 3.5%; $t_{19} = 2.054$, $P = 0.054$). The difference in false alarm rates between the no sound condition and the false reports of somatosensation on the opposite side of the sound also was not significant (3.5% vs. 2.8%; $t_{19} = 1.209$, $P = 0.241$).

Although the design of this experiment was not perfectly suited to conduct signal detection analyses, and not all response biases could be ruled out with this design, we nonetheless conducted signal detection analyses to obtain an estimate of bias free changes in sensitivity to somatosensory perception with sound. The *d'* values were calculated from the hit (correct localization of the somatosensory stimulus) and false alarm (see above and Table 1) rates for each subject and subjected to the same statistical analyses as the percent correct data. Consistent with the analyses on the discrimination and false alarm rates, an ANOVA revealed a significant difference in sensitivity between the three auditory stimulus conditions ($F_{1,19} = 7.05$, $P = 0.002$). There was significantly higher sensitivity for discriminating the side of the somatosensory stimulus when the sound was on the same side ($d' = 2.00$) as compared to the opposite side ($d' = 1.30$; $t_{19} = 3.689$, $P = 0.002$) and no sound conditions ($d' = 1.14$; $t_{19} = 3.352$, $P = 0.003$). There was no decrease in sensitivity when the sound was delivered to the hand opposite to the somatosensory stimulus as compared to the no sound conditions ($t_{19} = 0.561$, $P = 0.581$). These differences in d' values indicate that perceptual sensitivity, independent of any response or decisional biases, was enhanced when the somatosensory stimulus was on the same side as the auditory one.

There was also a marginally significant difference in criterion between the three main conditions ($F(1,19) = 2.99$, $P = 0.062$). In order to assess the source of this marginal effect, we conducted further paired *t*-tests on the *c* values, which should be interpreted with caution since the main effect did not achieve significance. On the trials when no somatosensory stimulus was delivered, participants were more likely to report feeling an illusory somatosensory stimulus on the same side as the sound ($c = 1.09$) as compared to the opposite side ($c = 0.84$; $t_{19} = 2.509$, $P = 0.021$) and no sound conditions ($c = 0.79$; $t_{19} = 2.243$, $P = 0.037$). There was no difference in response biases for the opposite side sound vs. no sound conditions ($t_{19} = 0.562$, $P = 0.581$).

The analyses of d' values indicate that a sound on the same side as the somatosensory stimulus significantly enhances discrimination, regardless of any response or decisional biases that may or may not have been present. Unlike any contributions from response biases, which should have mostly been ruled out by our signal detection analyses, these results could have been affected by an enhanced alerting, temporal marking, or attentional orienting effect from the sound that increased touch perception (cf. Spence et al. 1998). However, unlike the cross-modal attention studies by Spence, Driver, and colleagues (Driver and Spence 1998a, b), in which auditory stimuli preceded tactile ones, our stimuli were simultaneously presented, making an alerting, marking, or orienting account of our results less likely. We return to this issue in the General Discussion.

Sound on the opposite side from the cutaneous event did not produce a decrease or cost in its discrimination. Our previous work on vision and touch (Johnson et al. 2006), using a similar design and paradigm, revealed a large decrement in performance when a somatosensory stimulus was delivered to the opposite side from vision. This difference may be explained by the poorer spatial localization capabilities of the auditory as compared to the visual system, or the fact that the sounds were not emitted from the precise location of the electrical cutaneous stimuli (i.e., the middle finger of the hands).

Since auditory coding is more dependent on frequency-based information than precise spatial localization, the enhancing effects on somatosensory processing from audition may be more readily measured in the frequency-domain. Experiment 3 examined the effects of different frequencies of auditory information on somatosensory processing.

Experiment 3

This experiment used different frequencies of auditory and somatosensory stimuli to assess whether the effects of sounds on touch perception are frequency dependent. We hypothesized that the effects of sound on vibrotactile perception might be restricted to specific frequencies. Indeed, a recent study suggested that delayed auditory feedback at the same frequency as a vibrotactile stimuli improved tactile discrimination performance via acoustic imagery (Iguchi et al. 2007). In order to test our hypothesis, we used either congruent or incongruent frequencies of sound and touch in a two-alternative, forced-choice (2AFC) tactile discrimination paradigm. For Experiment 3, we developed a somatosensory stimulation apparatus that used piezoelectric vibrators to allow for precise control of vibrotactile stimulation frequency and to extend our results from the previous two experiments to other types of somatosensory stimuli.

Methods

After informed consent, 19 undergraduate students (9 males; 10 females; mean age = 19.9 years) participated in this experiment in exchange for course credit. All subjects reported having no auditory or somatosensory deficits.

Somatosensory stimuli were delivered using a piezoelectric bending element (bender). The bender was affixed to the dorsal surface of the left hand in each subject using a cloth bandage wrap. A 100 or 200 Hz sinusoidal voltage was applied to the bender, causing it to oscillate at one of these two frequencies. The duration of the oscillation was 250 ms, producing the percept of a brief “buzz” similar to that of a cell phone in vibrate mode. Because of the low intensity of the tactile stimulus and the further attenuation of any sounds from the bandage wrap, the piezoelectric bender did not produce audible vibrations (undetectable increase in sound pressure level as measured with a SPL meter).

For each subject, the amplitude of the applied voltage to the bender was adjusted to near-threshold levels and the perceived intensities of the two stimulation frequencies were equated. The voltage for the 100 Hz vibration was first adjusted to produce a moderately intense percept. Then, the 200 Hz and the 100 Hz vibrations were alternately presented as the subject adjusted the voltage of the 200 Hz vibration to match the perceived intensity of the 100 Hz vibration. This modified staircase procedure (with random initial voltages for the 200 Hz vibration) was performed three times, with the mean voltage used for the experiment.

The auditory stimulus, when delivered, was either a 100 Hz or a 200 Hz pure frequency tone (59 dB or 60 dB in intensity, respectively) delivered for 250 ms over a speaker placed 50 cm in front of the left hand. Thus, the auditory stimulus could either be congruent or incongruent with the tactile stimulus. The position and distance of the speaker from the hand was such that no air pressure was felt on the hand from the sounds. As in Experiments 1 and 2, the participants' left hands rested on the armrest of their chair.

A 3 sound (100 Hz, 200 Hz, or no sound) × 2 touch (100 Hz or 200 Hz) factorial design was used. The start of each trial was signaled by a white fixation cross that was presented for 500 ms at the center of a blank LCD monitor. The participants performed a 2-AFC task, reporting whether the tactile stimulus on each trial was the low (i.e., 100 Hz) or high (i.e., 200 Hz) tactile stimulus frequency, ignoring any auditory stimulation. Each subject performed 20 trials for each of the six conditions for a total of 120 trials. The data were collapsed across stimulation frequency, resulting in 40 trials for congruent auditory and tactile stimulation, 40 trials of incongruent auditory and tactile stimulation, and 40 trials for tactile stimulation with no auditory stimulus.

Results and discussion

When the sound was the same frequency as the touch, tactile discrimination performance increased by 12.8%, and when the sound was the opposite frequency as the touch, tactile discrimination performance *decreased* by 18.8% in comparison to the no sound condition (see Fig. 3 and Table 1). A two-way ANOVA with auditory stimulus (none, same frequency, different frequency) and vibrotactile frequency (100 Hz, 200 Hz) as the two within subject factors revealed a highly significant main effect of sound ($F_{1,18} = 21.008$, $P < 0.001$). This main effect was driven both by an increase in discrimination performance with congruent sounds as compared to the no sound conditions ($t_{18} = 3.010$, $P < 0.001$) and a decrease in performance with incongruent sounds as compared to the no sound conditions ($t_{18} = 4.442$, $P < 0.001$). The main effect of vibrotactile frequency ($F_{1,18} = 0.440$, $P = 0.516$) and the sound × tactile frequency interaction ($F_{1,18} = 1.434$, $P = 0.252$) were not significant. These results demonstrate a frequency-specific effect of sound on touch perception.

General discussion

Three experiments examined the effects of a task-irrelevant auditory stimulus on somatosensory perception. In Experiment 1, a simultaneously presented auditory stimulus

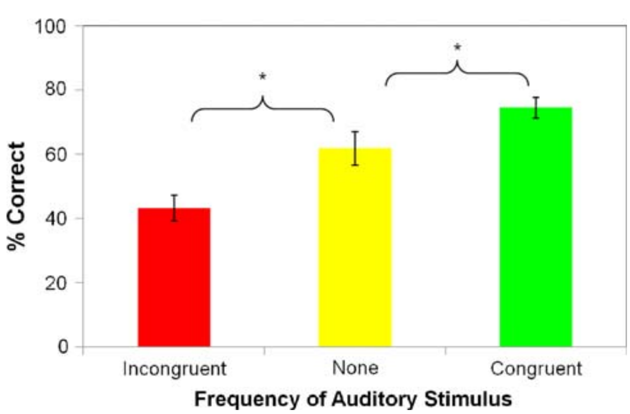

Fig. 3 The data from Experiment 3 examining frequency-specific effects of audition on touch. *Error bars* reflect ± 1 standard error of the mean

increased sensitivity to a near-threshold touch stimulus. Experiment 2 showed that the enhancing effects of sounds on touch perception are spatially specific; only sounds that occurred on the same side as the touch enhanced spatial discrimination. In Experiment 3, a somatosensory stimulus containing frequency was used to show that the effects of sound on touch are frequency-dependent: discrimination performance increased when a sound was the same frequency as the tactile stimulus and decreased when the sound was of a different frequency.

All three experiments showed a significant effect of sound on touch perception, even though different experimental paradigms were used. This consistency is important because it demonstrates the robustness of the auditory influences on touch perception, and suggests that there are likely to be a variety of interesting neural interactions underlying these behavioral effects. For instance, Experiment 1 shows that simultaneous sound enhances somatosensory perception, with the increases in d' indicating that the effect is not due to a response bias. However, the results of Experiment 1 could have been due to an increase in arousal, which could arise from a simultaneous stimulus in any modality (not necessarily auditory–somatosensory). However, Experiment 2 shows that the interaction between audition and somatosensation is spatially lateralized, with signal detection analyses confirming that this lateralized enhancement was not solely a consequence of a response bias. These results suggest neural interactions occurring in brain regions that have spatial maps and indicate that these effects are not an effect on general arousal. The fact that performance was worse in Experiment 2 than Experiment 1 is relatively uninformative because subjects performed a more difficult discrimination task (deciding between two hands) as opposed to the simple detection task (on only one hand) in Experiment 1.

Although there was no correspondence between somatosensory frequency and auditory frequency in the first two experiments, the onset of the electrical cutaneous stimulus used in those experiments coincided with the onset of the auditory stimulus and auditory–somatosensory interactions were observed. Unlike Experiments 1 and 2, Experiment 3 used piezoelectric vibrotactile stimulation of much longer temporal durations and specific frequencies. However, due to potential variations in mechanical inertia of the stimulators and the skin, the mechanical deflection of the vibrotactile device may not have been precisely in phase with the sound. Nonetheless, the use of a vibrotactile stimulus allowed us to study auditory–tactile interactions in the frequency domain, which is more precisely coded by the auditory and somatosensory systems, and robust auditory–tactile interactions were measured. This suggests that there may be three separate dimensions along which auditory–tactile multisensory integration may occur (temporal synchrony, spatial concordance, and frequency concordance). In future studies, it will be important to explore these dimensions. For instance, is the integration between spatially congruent and frequency congruent auditory–tactile stimuli additive and do harmonics of the sounds produce similar effects on vibrotactile frequency discrimination?

These systematic effects of sound on touch perception may be a consequence of neuronal interactions within and between several different brain areas. The organization of the cerebral cortex is well suited for integrating sound and touch information since (a) primary auditory cortex is adjacent to secondary somatosensory areas, (b) there are anatomical connections from somatosensory cortex into auditory cortex (Schroeder et al. 2001), (c) functional imaging studies show common cortical activation sites for auditory and somatosensory information (Foxe et al. 2002; Ozcan et al. 2005; Schurmann et al. 2006; Beauchamp and Ro 2008), and (d) even unisensory cortex may be driven by different sensory modalities (Macaluso and Driver 2005; Ghazanfar and Schroeder 2006). This anatomical proximity and functional interconnectivity may provide the neural basis for the interactions between audition and touch measured in these experiments; connections between nearby areas of cortex are more extensive than connections between distant areas.

The interactions between the auditory and somatosensory systems may reflect a special case of multisensory integration for information in peripersonal space. Previous studies have shown that auditory–somatosensory interactions may be specific to information around the body (Serino et al. 2007), regardless of whether the peripersonal auditory information comes from in front of or behind the subject (Farne and Ladavas 2002; Zampini et al. 2007). Since in our experiments the auditory information was always presented through headphones or in peripersonal space, we cannot assess whether the increases in sensitivity to somatosensory information would also extend for auditory information in far, extrapersonal space. Further experiments directly modulating the distance of the auditory information, as well as the intensity (Occelli et al. 2008), might be informative regarding some of the boundary conditions of these enhancing effects on somatosensation from audition.

It is important to note that our experiments used simultaneous auditory and tactile stimuli. Therefore, it is unlikely that our results are a consequence of a spatial orienting of attention effect of the sound on touch, as has been shown in other studies (cf. Spence and Driver 1997). In contrast to spatial orienting, which requires some time for attention to move to the locus of an event (Posner 1980), our results could have been influenced by an increased level of general alerting and/or arousal when an auditory stimulus was presented. However, the fact that the enhancements of touch from sound were spatially- and frequency-specific rather than more generally enhancing suggests that a general alerting or arousal account for these results is insufficient. In some of our previous work, we have also demonstrated that a simultaneous visual stimulus can affect tactile processing in similar ways (Johnson et al. 2006). Taken together, these findings suggest that these multisensory enhancement effects may be a result of super-additive processing of vision, audition, and touch in brain areas coding for all of these sensory modalities (e.g., the superior colliculus and the posterior parietal cortex). We are currently examining these enhancing effects of sound on touch using functional magnetic resonance imaging, which may provide further clues to the neural mechanisms underlying these effects.

Recently, we reported a patient with an interesting linkage between touch and sound (Ro et al. 2007). Following a thalamic stroke, the patient had somatosensory processing deficits on the left side of her body. Gradually, the patient came to feel touches when she heard certain sounds. A possible explanation for these results is that latent connections from auditory cortex to somatosensory cortex are now hyperactive, as further suggested by functional neuroimaging experiments on this patient (Beauchamp and Ro 2008). Sounds that produced somatosensory percepts activated somatosensory cortex, which result in the perceptions of touch. The results from this patient further support a tight link between sound and touch, and suggest some degree of crosstalk between these two sensory modalities.

In addition to demonstrating some of the ways in which sounds interact with touch perception, the current results suggest another systematic and more general medium through which multisensory information might be integrated. Specifically, our studies extend the work demonstrating spatial and temporal specificity in multisensory integration and attention (e.g., see Stein and Meredith 1993; Driver and Spence 1998b; Driver and Noesselt 2008) into the frequency domain. By integrating information from different sensory modalities based on stimulus frequency, perception might be further optimized through this frequency-specific form of multisensory integration. Further work examining frequency-dependent visual-auditory and visual-tactile integration may provide the boundary conditions for multisensory interactions based on frequency information.

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