

Research Article

Multisensory Integration

Central Processing Modifies Peripheral Systems

J.E. Lugo,¹ R. Doti,¹ Walter Wittich,² and Jocelyn Faubert¹¹University of Montreal and ²McGill University

ABSTRACT—*Multisensory integration in humans is thought to be essentially a brain phenomenon, but theories are silent as to the possible involvement of the peripheral nervous system. We provide evidence that this approach is insufficient. We report novel tactile-auditory and tactile-visual interactions in humans, demonstrating that a facilitating sound or visual stimulus that is exactly synchronous with an excitatory tactile signal presented at the lower leg increases the peripheral representation of that excitatory signal. These results demonstrate that during multisensory integration, the brain not only continuously binds information obtained from the senses, but also acts directly on that information by modulating activity at peripheral levels. We also discuss a theoretical framework to explain this novel interaction.*

The traditional view of multisensory integration (MI) is that it involves cortical integration of information from two or more sensory signals. Because multisensory stimuli that are spatially and temporally coincident and carry congruent information are likely to be derived from the same event, they typically result in behavioral, perceptual, or both behavioral and perceptual enhancements (Laurienti, Burdette, Maldjian, & Wallace, 2006). Additional support for the role of central information processing in MI comes from studies demonstrating the McGurk effect (McGurk & MacDonald, 1976) and the ventriloquism effect (Thurlow & Rosenthal, 1976), which show that cognitive processes can give rise to new percepts containing information that was not present in the peripheral stimulus. There now exists a substantial literature detailing how multisensory interactions shape behavior and perception in humans (Calvert, Spence, & Stein, 2004; Laurienti et al., 2006; Stein & Meredith, 1993). What is still poorly understood is whether these cortical

mechanisms also have the ability to affect peripheral systems through distributed conditioning mechanisms (e.g., feedback).

Efficient integration of multisensory inputs requires temporal coincidence, which naturally happens when the same signal is applied simultaneously to different senses (Calvert et al., 1997; Jousmaki & Hari, 1998; Lakatos, Chen, O'Connell, Mills, & Schroeder, 2007; Macaluso, Frith, & Driver, 2000; Schurmann, Caetano, Jousmaki, & Hari, 2004). Researchers interested in MI have studied tactile-auditory (Calvert et al., 1997; Jousmaki & Hari, 1998; Schurmann et al., 2004) and tactile-visual (Macaluso et al., 2000) interactions in humans. For example, in the parchment-skin illusion, a sound that is synchronous with hand rubbing strongly modifies the tactile sensations (Jousmaki & Hari, 1998). It has been proposed that MI occurs at a central level, where projections of different senses are integrated (Jousmaki & Hari, 1998; Macaluso et al., 2000). Furthermore, the greatest multisensory-mediated effects are generally seen when the individual stimuli are weak in eliciting a response on their own (Laurienti et al., 2006; Stein & Meredith, 1993; Wallace, Wilkinson, & Stein, 1996). That is, information from multiple sensory channels is likely to be most useful when the signals are ambiguous. This conclusion is known as the *inverse-effectiveness rule* and has significant physiological correlations in the superior colliculus.

However, there is an MI phenomenon that cannot be described by the inverse-effectiveness rule: *threshold cross-modal stochastic resonance (SR)*. SR is a counterintuitive phenomenon in which a particular level of noise enhances the response of a nonlinear system, such as the perceptual system of a living creature, to a weak input signal (Wells, Ward, Chua, & Inglis, 2005). A simple variant of SR is threshold SR, which results from the concurrence of a subthreshold stimulus and noise; when noise and signal are at an optimum ratio, the threshold crossings probabilistically follow the amplitude modulations of the signal (threshold crossings are more likely when the signal level is nearer the threshold and less likely when it is farther away), providing information about its nature. The signature of SR is that when the threshold signal-to-noise ratio, which is proportional to the system's sensitivity, is plotted as a function of

Address correspondence to Jocelyn Faubert, Visual Psychophysics and Perception Laboratory, School of Optometry, University of Montreal, C.P. 6128 succ. Centre Ville, Montreal, Quebec, Canada H3C 3J7, e-mail: jocelyn.faubert@umontreal.ca.

noise level, the resulting graph has an inverted-U shape. It has been proposed that SR is a particular case of a more general pattern of dynamics; in some instances, a given system will exhibit deterministically induced resonances (i.e., when the evolution of the stimulus over time is known exactly), but in other instances, it will exhibit stochastically induced resonances (i.e., when the evolution of the stimulus over time is random; Simiu, 2002). For example, the auditory nerve fibers exhibit deterministic resonances at very specific frequencies, but exhibit SR in other cases.

Threshold cross-modal SR, demonstrated in recent studies, is an SR-like phenomenon involving auditory-visual (Faubert, Hahler, Doti, & Lugo, 2007; Lugo, Doti, & Faubert, 2008; Manjarrez, Mendez, Martinez, Flores, & Mirasso, 2007), auditory-tactile (Faubert et al., 2007; Lugo et al., 2008), and auditory-proprioceptive (Faubert et al., 2007; Lugo et al., 2008) interactions. In general, sensitivity in detecting a weak visual, tactile, or proprioceptive signal was an inverted-U-shaped function of the intensity of auditory noise that was presented concurrently with the signal. These results are inconsistent with the inverse-effectiveness rule, but consistent with recent results (Ross, Saint-Amour, Leavitt, Javitt, & Foxe, 2007) showing that during speech comprehension in noisy environments, auditory-visual MI yields optimal performance at a particular intermediate level of auditory noise.

Here we report novel tactile-visual and tactile-auditory interactions in humans. We hypothesized that the central integration of stimuli across sensory modalities would increase a peripheral tactile signal through conditioning from the brain. We show that an auditory or visual signal that is exactly synchronous with a subthreshold tactile signal enhances the tactile perception, and the tactile signal becomes suprathreshold. Furthermore, the peripheral electrical representation (electromyography, or EMG) of that subthreshold tactile stimulus also increases when the auditory or visual signal is present, which shows that there is a relationship between the enhancement of tactile perception and this increment in EMG activity. These results demonstrate that during MI, the brain not only continuously binds information obtained from the senses, but also acts directly on that information by modulating activity at peripheral levels. Moreover, we believe that the dynamics of this novel interaction are similar to the dynamics of SR, as they can be described by an inverted-U-shaped function.

GENERAL METHODOLOGY

This study received approval from the Institutional Review Board of the University of Montreal. We performed EMG measurements in a sample of 5 healthy subjects (25–52 years old) with no history of auditory, tactile, visual, or other detectable neurological disorders. The subjects' vision was normal or corrected to normal, and we tested all subjects and confirmed that they had normal hearing. The experiments took place in a dark

room. Subjects were seated with their forearms supported on their thighs. An electrical signal was applied to the subjects such that at a certain amplitude level, the signal evoked a tactile sensation in all the subjects. Individual tactile thresholds were established with the method of limits (average of 10 upper and 10 lower limits). The tactile thresholds were determined individually for each subject and ranged from 29 to 32 V (± 0.25 V).

In Experiment 1, every subject was tested in three sessions; in Experiments 2 through 4, subjects were tested in a single session; and in Experiment 5, they were tested in five sessions. Each session consisted of 10 trials. On each trial, we obtained two paired measurements: the EMG for a tactile stimulus at a subthreshold level with a fixed amplitude (1.5% below threshold, about 0.5 V) and the EMG for a tactile stimulus that either increased in amplitude or was presented concurrently with a stimulus in another modality, depending on the experiment. In Experiment 1, to study tactile interactions, we used a tactile stimulus that was subthreshold (1.5% below threshold) and directly increased the amplitude of the electrical signal to three suprathreshold levels (15%, 35%, and 68% above threshold). Experiment 2 examined tactile-visual interactions by using a subthreshold tactile stimulus (1.5% below threshold) that was presented concurrently with a clearly visible stimulus, and Experiment 3 studied tactile-auditory interactions by using a subthreshold tactile stimulus (1.5% below threshold) that was presented concurrently with a clearly audible stimulus. Experiment 4 studied interactions between a tactile stimulus and auditory noise; in this experiment, a subthreshold tactile stimulus (1.5% below threshold) was presented concurrently with a clearly audible noise stimulus (rather than the deterministic auditory stimulus used in Experiment 3). Finally, in Experiment 5, a subthreshold tactile stimulus (1.5% below threshold) was presented concurrently with an auditory stimulus at one of five suprathreshold levels. Every EMG measurement lasted 30 s, and the order of the paired measurements within each trial was randomized to ensure that the observed effects were not simply due to a generalized modulation in attention or arousal. Figure 1 depicts the nine components of the experimental setup, and Figure 2a shows the physical paths of the sensory signals from the equipment to the brain.

Electrical Signals

Repetitive deterministic biphasic signals (see Fig. 2b) were generated with a solid-state square-wave stimulator (Grass S48; like the other equipment listed in this paragraph, from Astro-Med, Inc., Longueuil, Quebec, Canada) and a stimulus isolation unit (SIU5; Components 1 and 2 in Fig. 1). The current at the output of the stimulus isolation unit was 1 mA. The frequency was 1 Hz, with an active period of 100 ms. We used two Ag-AgCl electrodes (Grass F-E9-60-5) to introduce the signal (Component 8). The electrodes were filled with electrode gel (Grass EC60) and were separated by 10 cm.

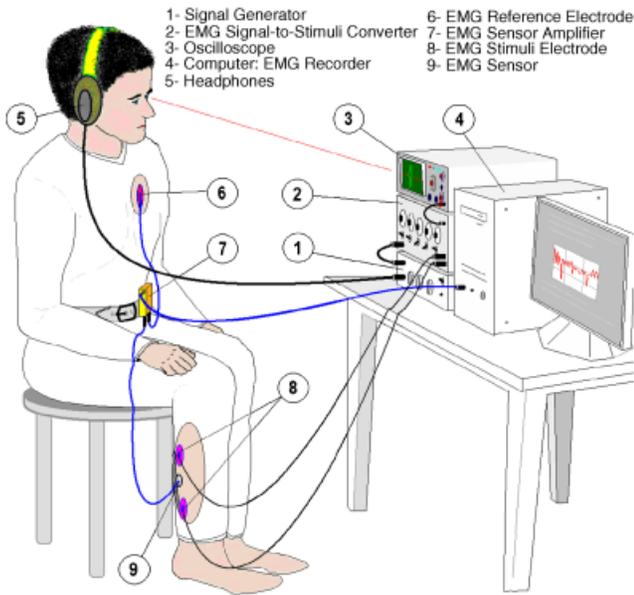


Fig. 1. The nine components of the experimental setup. EMG = electromyogram.

EMG Measurements

Electrical signals were delivered to the right calf (gastrocnemius medial head). One differential EMG electrode (Bagnoli-2 EMG system, Delsys Inc., Boston, MA) was placed between the two Ag-AgCl electrodes (Component 9), and one reference electrode (Delsys Inc., Boston, MA) was placed at the left pectoralis major (Component 6). Both the differential and the reference elec-

trodes were connected to an amplifier (set to a gain of 1,000) with a sampling frequency of 1000 Hz (Component 7). The EMG signals were stored for further analysis (Component 4).

Tactile-Visual Trials

The biphasic visual signal (Component 3) was displayed on an oscilloscope (Kikusui COS6100) and looked like a dot expanding to a line, first up and then down (see Fig. 2c). The luminance level of the oscilloscope screen was 8 cd/m². The level of luminance was measured by placing a photometer (Minolta CS-100, Konica Minolta Sensing Americas, Inc., Ramsey, NJ) at viewing distance from the oscilloscope screen and then displaying a fixed dot at the center of the screen. The amplitude of the visual signal was displayed on the oscilloscope. The vertical control was set to 20 mV/div, and the time-base control was off. The visual and tactile signals were applied simultaneously. All subjects were seated 45 cm from the oscilloscope screen and were asked to look at the screen and report when they first felt a tactile sensation. Once the subjects reported a change in tactile sensation, the EMG measurements started.

Tactile-Auditory Trials

The auditory stimuli were presented binaurally by means of a pair of high-precision headphones (SR80, Grado Labs, Inc., New York, NY; Component 5 in Fig. 1). To characterize the auditory stimuli, we used the applied peak voltage at the exit of an amplifier (RA62b, Rolls Corp., Salt Lake City, UT), instead

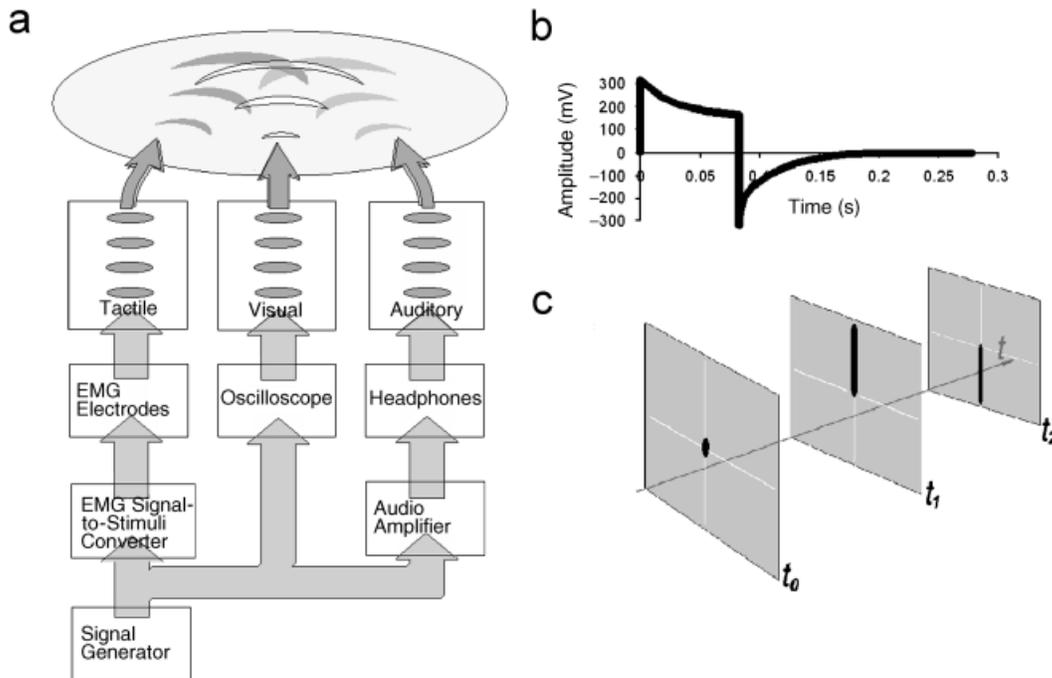


Fig. 2. Physical signals and layout of the signal paths in the experiments: (a) the physical paths leading the signals to the brain, (b) the electrical signal's physical form, and (c) the visual stimulus (a center dot that expanded to a line, first upward and then downward). The symbols t_0 , t_1 , and t_2 represent a temporal sequence. EMG = electromyogram.

of the sound-pressure level into the aural cavity, both because the measurement is simple and reliable and because the experimental values are easily replicated with high-precision headphones. We used a calibrated high-fidelity capacitor microphone (ECM8000, Behringer Canada Ltd., Seattle, WA) to verify the frequency response of the headphones inside an acoustically isolated chamber. The sound disturbances in the testing room (e.g., computer fans and low-power sounds coming from outside the room) were recorded using the same microphone, and their upper-bound frequency was 2.5 kHz at an intensity of 50 ± 3.5 dB. We evaluated the subjects' hearing from 250 Hz to 8 kHz using an audiometer (Midimate 602, Madsen Electronics, Minneapolis, MN); these evaluations were conducted in a 6-ft \times 10-ft double-wall audiometric sound suite (Industrial Acoustics Co., New York, NY) that met the American National Standards Institute (ANSI) standard (Standard 3.1-1991) for permissible ambient noise levels (in one-third-octave bands) for testing in free-field conditions with headphones. During the experimental trials, all subjects were seated and were asked to listen to the sound in the headphones and report when they first felt a tactile sensation. Once the subjects reported a change in tactile sensation, the EMG measurements started.

Data Analysis

After the data were collected, the power spectral density (PSD) of each EMG measurement was obtained. To calculate the normalized PSD for each condition, $\Psi_N(\omega)$ (where ω is the frequency in hertz), we divided the PSD at the suprathreshold level by the corresponding PSD at the subthreshold level on each trial and then averaged across trials. The normalized PSD was used to calculate the integral signal-to-noise ratio (integral SNR), defined as follows:

$$\text{Integral SNR} = \int_{-\infty}^{\infty} \Psi_N(\omega) \Theta d\omega / \int_{-\infty}^{\infty} \Theta d\omega, \quad (1)$$

where Θ is a step function that equals 0 when $\Psi_N(\omega) < 1$ and equals 1 otherwise. We used only $\Psi_N(\omega)$ values equal to or

greater than 1 because the energy associated with tactile sensation necessarily results in a value within this range, and values lower than 1 indicate a loss of energy (noise—i.e., the energy in the facilitatory stimulus was not used for the tactile stimulus to become suprathreshold). An integral SNR greater than 1 means that there was an energy transfer from the visual or auditory signal to the tactile signal. Given the electrical signal (Fig. 2b), the EMG signal was lower and upper bounded; therefore, the integrals defined in Equation 1 existed. To analyze the data, we used the method proposed by Killeen (2005), calculating the d' probability of replication, p_{rep} , rather than p values. To calculate p_{rep} , we used the average as the dependent measure and derived the standard deviation from the integral SNR and a homogeneous distribution with an average of 1 and standard deviation of 0 as a control. The experimental and control sample sizes were both 10. With this information, the effect size d' and the standard deviation of replication, σ_{rep} , were calculated. The value of p_{rep} was computed by obtaining the probability of the variable formed by the ratio of d' and σ_{rep} , assuming that this variable followed a standard normal distribution.

RESULTS

Experiment 1: Tactile Stimulation, EMG Activity, and Corresponding Sensations

First, we investigated how tactile perception and the corresponding EMG activity was affected when we increased the amplitude of the electrical signal. As we increased the electrical signal, the EMG activity increased correspondingly, primarily in frequencies between 250 and 380 Hz. Figure 3a displays the EMG results from 1 subject. Figure 3b shows the integral SNR for the same subject; as expected, its value increased with voltage. We did not expect that this unimodal effect would be the same as a cross-modal interaction, but the mechanism underlying the transition from subthreshold to suprathreshold could be the same. That is, in both cases, the transition could be determined by the energy content of the signals (and probably the

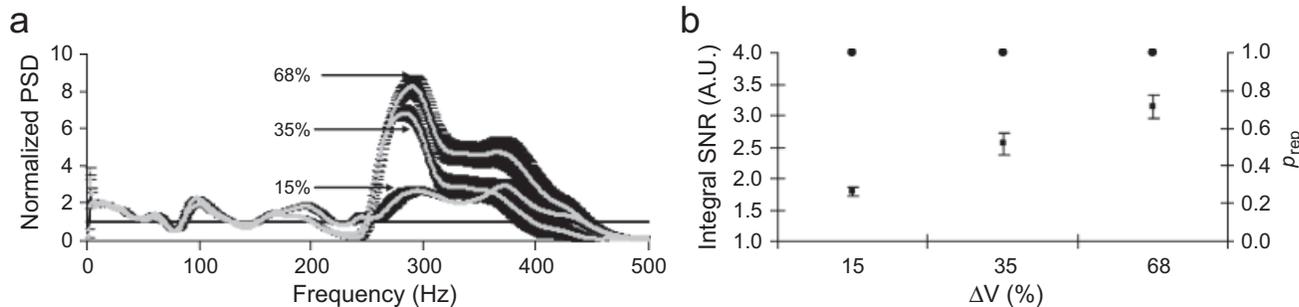


Fig. 3. Results from Experiment 1: tactile response to deterministic signals. The graph in (a) presents the normalized power spectrum densities (PSDs) for 1 subject (S3). The three functions represent the electromyographic (EMG) response to direct stimulation 15%, 35%, and 68% above a subthreshold signal (1.5% below threshold). The gray lines represent the average, and the black shading represents 1 SE. The graph in (b) presents the integral signal-to-noise ratio (SNR; left y-axis) for the three normalized PSDs for this same subject as a function of the amplitude of the electrical signal; these results are represented by the black dots with error bars. Error bars correspond to 1 SE. A.U. = arbitrary units. The black dots without error bars indicate d' replication probabilities (right y-axis).

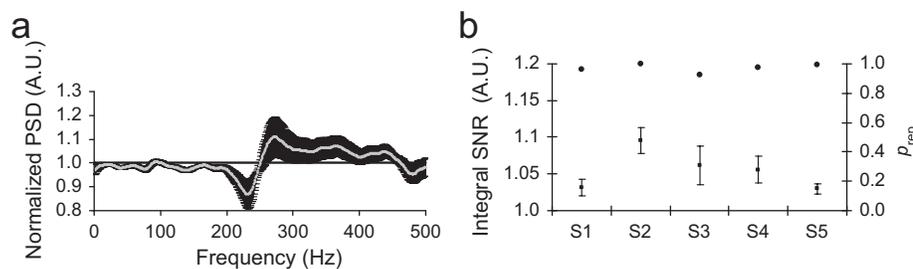


Fig. 4. Results from Experiment 2: tactile-visual interaction with deterministic signals. The graph in (a) presents the normalized power spectrum density (PSD) for 1 subject (S3). The gray line represents the mean, and the black shading represents 1 *SE*. The graph in (b) shows the integral signal-to-noise ratio (SNR; left y-axis) for each of the 5 subjects; these results are represented by the black dots with error bars. Error bars correspond to 1 *SE*. A.U. = arbitrary units. The black dots without error bars indicate d' replication probabilities (right y-axis).

frequency content as well). We began with a subthreshold signal and then, by transferring more energy to the system, produced a transition to suprathreshold stimulation that correlated with increments in a range of EMG frequencies. To clarify and gain a more fundamental understanding of this phenomenon, we also explored tactile-visual and tactile-auditory interactions.

Experiment 2: Tactile-Visual Interactions

Second, we investigated how tactile perception and the corresponding EMG activity were affected when the amplitude of the tactile stimulus was subthreshold (1.5% below threshold) and a suprathreshold visual stimulus was presented concurrently. The visual stimulus augmented tactile perception and the corresponding EMG activity. When we introduced the visual stimulus, the EMG activity increased correspondingly, primarily in frequencies between 290 and 380 Hz (Fig. 4a displays the EMG results from 1 subject). The results for tactile-visual interaction were similar to those for tactile interaction in the sense that some peaks of the average EMG signal coincided with peaks obtained in Experiment 1 (e.g., the peaks centered at 290 and 380 Hz; see Fig. 4a). Figure 4b shows the integral SNR for all subjects, which ranged from approximately 1.03 (increase of 3% relative to baseline) to 1.1 (increase of 10%). As in Experiment 1, the increment in EMG activity (represented by the increment in the integral SNR) could have been determined by the energy content of the signals (and probably by the frequency content as well).

Experiment 3: Tactile-Auditory Interactions

Next, we studied tactile-auditory interactions, using auditory signals with a fixed amplitude of 9 mV (peak voltage) at the amplifier exit. Figure 5a shows an example of the normalized PSD. The integral SNR values for tactile-auditory interaction were, in general, smaller than those obtained for tactile-visual interaction (see Fig. 5b); the value for only 1 subject was greater than 1.03 (increase of 3% relative to baseline). If we assume that the efficiency of energy transfer is the same for tactile-visual and tactile-auditory interactions, then these results suggest that the

energy transfer was lower for tactile-auditory interaction than for tactile-visual interaction. Furthermore, the frequencies at which the EMG increased were not in all cases the same as the frequencies at which the EMG increased for tactile and tactile-visual interactions. Nevertheless, these results do not preclude the possibility that the integration of representations of tactile and auditory signals extends from central to peripheral systems.

Can we explain the results of Experiments 2 and 3 in terms of MI? The first condition for MI, temporal synchronicity, was satisfied in our experiments, because the two stimuli were presented at the same time. However, because the visual and auditory stimuli were suprathreshold and the tactile stimuli were subthreshold, the inverse-effectiveness rule seems not to be applicable to this case (greatest multisensory-mediated effects are generally seen when the individual stimuli are both weak in eliciting a response on their own). Instead, these results are congruent with those of recent studies of threshold cross-modal SR (Faubert et al., 2007; Lugo et al., 2008; Manjarrez et al., 2007) and MI in the presence of noise (Ross et al., 2007). Therefore, we predicted (a) that visual or auditory noise also enhances tactile sensations, and (b) that there is a particular intermediate level of visual or auditory stimulation at which tactile-visual or tactile-auditory MI is optimally enhanced. We tested these predictions in Experiments 4 and 5 using auditory stimuli only.

Experiment 4

First, we tested tactile-auditory interaction using auditory noise instead of a deterministic auditory signal. In this experiment, we tested only the 3 subjects whose results for tactile-auditory interactions were similar. A computer provided auditory white noise to the amplifier. The amplitude of the white-noise signal was fixed at a value of 9 mV (peak voltage). Headphones and the human auditory system dramatically modify the spectrum density of white noise because of electromechanical resonances. Therefore, the brain cannot reproduce the full white-noise spectrum, but it still has an effective acoustic noise spectrum (ENS). We estimate that the ENS upper bound is around 15 kHz.

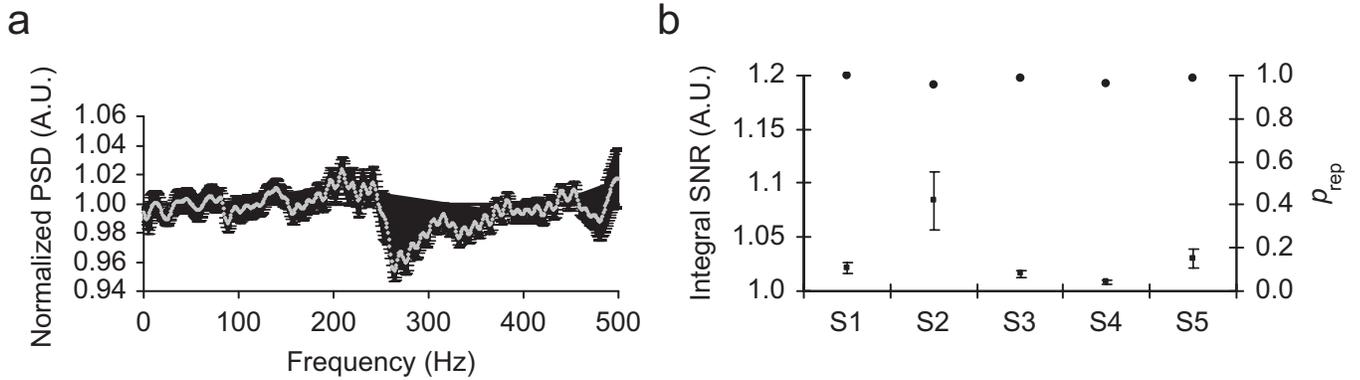


Fig. 5. Results from Experiment 3: tactile-auditory interaction with deterministic signals. The graph in (a) presents the normalized power spectrum density (PSD) for 1 subject (S3). The gray line represents the mean, and the black shading represents 1 SE. The graph in (b) shows the integral signal-to-noise ratio (SNR; left y-axis) for each of the 5 subjects; these results are represented by the black dots with error bars. Error bars correspond to 1 SE. A.U. = arbitrary units. The black dots without error bars indicate d' replication probabilities (right y-axis).

Figure 6a indicates that the auditory noise enhanced tactile sensations because, on average, the EMG signal increased when the auditory noise was present. In addition, the integral SNR (see Fig. 6b) ranged from 1.05 (increase of 5% relative to baseline) to 1.10 (increase of 10%; similar to the range of tactile-visual SNRs), indicating that the energy transfer of the auditory noise was bigger than the energy transfer of the deterministic auditory signal. These differences in energy transfer could have been due to the fact that the frequency content was larger in the auditory noise signal than in the auditory deterministic signal. This would imply that the frequency content, and not just the energy content, is important in inducing transitions in tactile perception. Clearly, Experiments 1 through 4 differed in the number of peak frequencies observed, but the underlying processing of the interactions appears similar.

Experiment 5

Second, we tested tactile-auditory interaction using deterministic auditory signals with different amplitudes and measured

EMG activation in 1 subject (S4). A different amplitude of the auditory signal was tested at each session. The six amplitudes were 0, 8, 12, 20, 30, and 300 mV (peak voltage) at the amplifier exit. To show the inverted-U-shaped function, we chose the upper limit to be 300 mV. We kept the intensity of the continuous auditory stimulus constant within each session and varied the intensity (in random order) between sessions. The order of the paired measurements was randomized within each trial (as in the previous experiments), and the order of the sessions was also randomized; this randomization ensured that the observed effects were not simply due to a modulation in attention or arousal.

Figure 7 shows three examples of the integral SNR. The graph for the full frequency range (Fig. 7a) demonstrates that as we increased the amplitude of the auditory stimulus, EMG activity increased, reached a maximum, and then decreased (inverted-U-shaped function). This implies that there is indeed a particular intermediate level of auditory stimulation at which tactile-auditory MI is optimally enhanced. Surprisingly, the same pattern of results shown in Figure 7a has been demonstrated in systems that show SR, deterministic resonance, or both (Simiu,

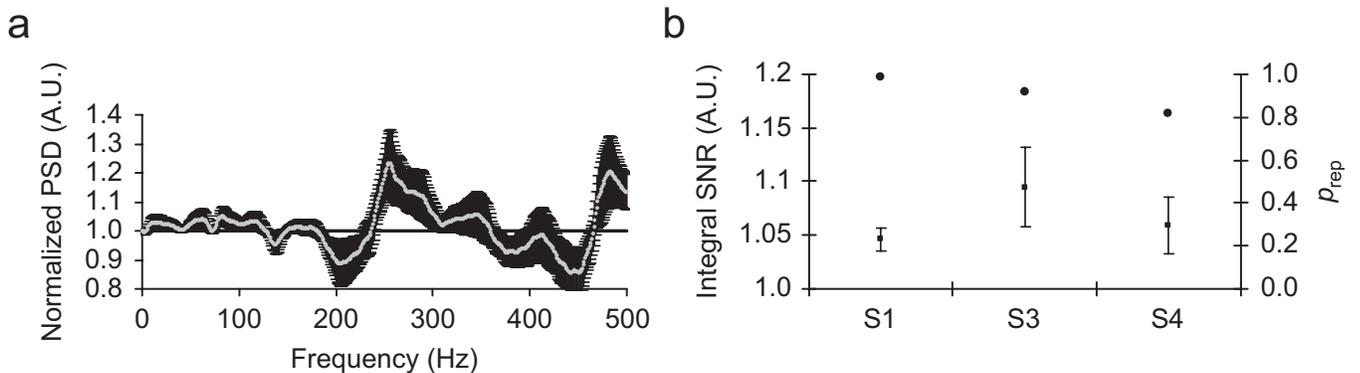


Fig. 6. Results from Experiment 4: tactile interactions with auditory noise. The graph in (a) presents the normalized power spectrum density (PSD) for 1 subject (S3). The gray line represents the mean, and the black shading represents 1 SE. The graph in (b) shows the integral signal-to-noise ratio (SNR; left y-axis) for each of the 3 subjects; these results are represented by the black dots with error bars. Error bars correspond to 1 SE. A.U. = arbitrary units. The black dots without error bars indicate d' replication probabilities (right y-axis).

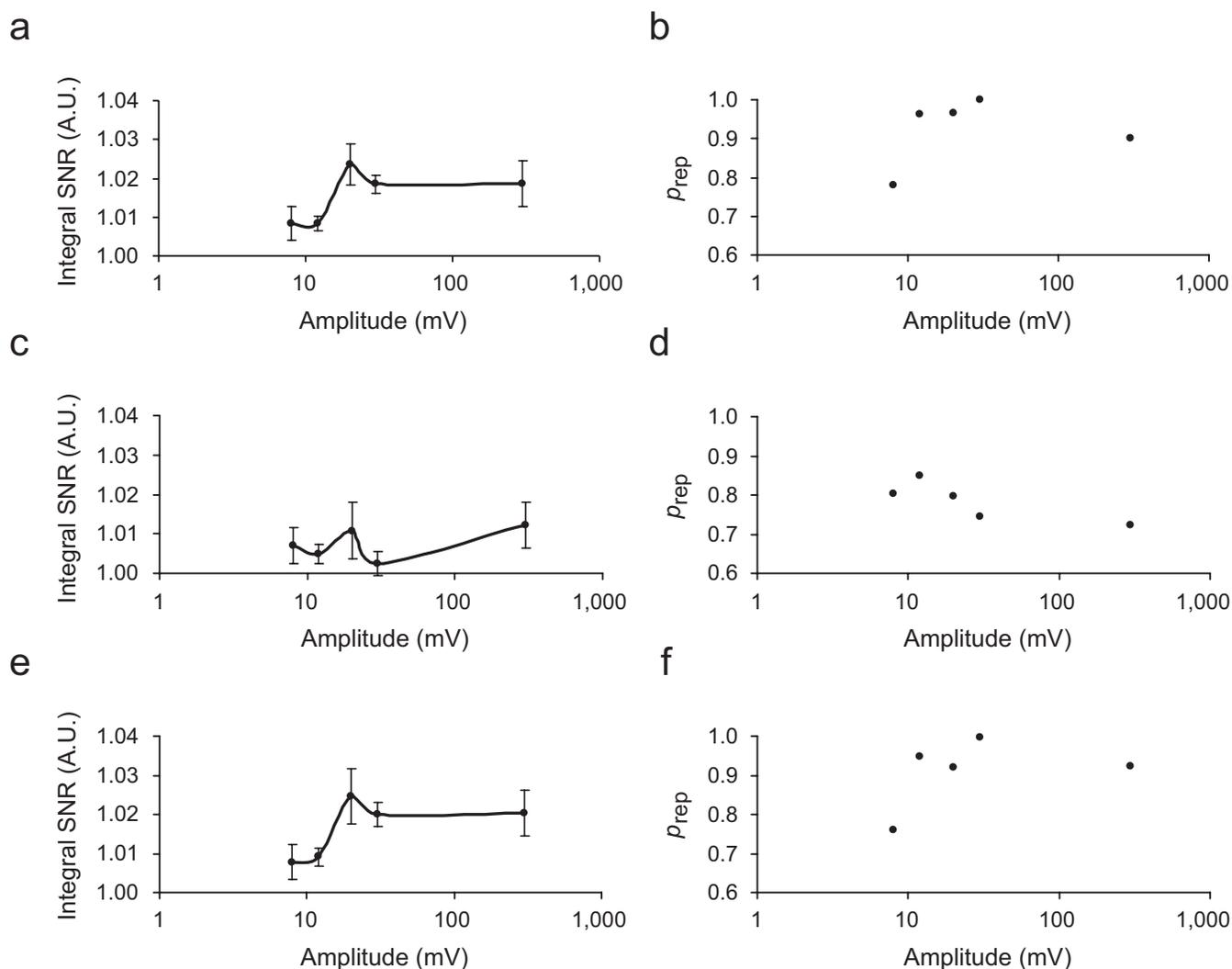


Fig. 7. Results from Experiment 5: tactile-auditory interactions with deterministic auditory signals at different amplitudes. The integral signal-to-noise ratio (SNR) of 1 subject (S4) is shown for the full frequency range of the electromyographic signal, from 0 through 500 Hz (a), and for two partial ranges, from 0 through 100 Hz (c) and from 100 through 500 Hz (e). Integral SNR is plotted as a function of amplitude of the auditory signal (amplitudes of 8, 12, 20, 30, and 300 mV only). Error bars correspond to 1 SE. The graphs in (b), (d), and (f) present corresponding d' replication probabilities.

2002). In the graph for the partial frequency range from 0 to 100 Hz (Fig. 7c), the inverted-U shape is not fully developed, a result that highlights the fact that the EMG signal does not increase at low frequencies and the optimal tactile sensation is not associated with this frequency interval. This fact is even more evident when one looks at the graph for the frequency interval from 100 to 500 Hz (Fig. 7e), which again shows the inverted-U shape. Figures 7b, 7d, and 7f show the d' replication probabilities for all the amplitudes. Interestingly, these values are lower for the lower frequencies than for the full spectrum and the higher frequencies.

GENERAL DISCUSSION

The present study investigated whether the signal of a sub-threshold tactile stimulus can be augmented by synchronous

auditory or visual signals, as well as auditory noise. We demonstrated that signals in the peripheral nervous system can be modulated by cross-modal interaction at the central level. We propose that the data presented here and other recent findings (Faubert et al., 2007; Manjarrez et al., 2007; Ross et al., 2007) can be explained in a theoretical framework along the same lines as described by Lakatos et al. (2007) and Macaluso et al. (2000). Macaluso et al. were the first to propose that cross-modal interactions occur at two levels of processing: first, there is processing at the level of biology, where the integration of important combinations of sensory stimuli produces behavioral effects, and second, there is processing at the level of physics, where the integration effects are the result of the signals that physically modulate the activity of visual neurons (e.g., in tactile-visual interactions, the tactile signals are carried by multisensory neurons projecting from the parietal areas of the somatosensory

cortex back to the primary visual cortex). The importance of this model is that it indicates that physical concepts, such as energy modulation, cannot be neglected in studying cross-modal interaction. This conclusion is also supported by the fact that integration of different but related sensory stimuli does not always require the glue of attention or awareness (de Gelder, 2000).

Recent experiments in awake macaques revealed clear somatosensory-auditory interactions, with a novel mechanism: Somatosensory inputs appeared to reset the phase of ongoing neuronal oscillations, so that accompanying auditory inputs arrived during an ideal, high-excitability phase and produced amplified neuronal responses (Lakatos et al., 2007). In contrast, responses to auditory inputs that arrived during the opposing low-excitability phase tended to be suppressed. We are proposing that a subthreshold excitatory signal (entering in one sense) that is synchronous with a facilitation signal (entering in a different sense) can be increased up to a resonant-like level and then decreased as a function of the energy level of that facilitation signal. Indeed, the energy and frequency content of the facilitation signal induces the transition in perception of the tactile signal. However, we are not proposing that the sensory activity is only peripheral. Initially, the energy level of the peripheral activity is not high enough to be detected by the central system; therefore, there is no interaction between central and peripheral systems at that time. When the facilitation signal enters the central system, it generates an activation that goes all the way back and modifies the original peripheral activity. The result is an activation that promotes resonance-like behavior, increasing the peripheral signal up to a level where it is perceived by the central system. This means that once the peripheral signal is perceived, the integration is represented not only at a central level, but also at a peripheral level. At some energy level of the facilitating stimulus, the peripheral activity reaches a maximum, and peripheral activity begins to decrease if the energy is increased further (see Fig. 7).

Because the increase in peripheral activity comes from the way the brain processes the energy and frequency content of the facilitation signal in each individual, the nature of the signals (deterministic or stochastic) involved in the interactions is not important. If the facilitation signal has the right energy and frequency content, the phenomenon will occur. That is why deterministic signals (visual or auditory) and a stochastic signal (auditory noise) demonstrated the same effects in our experiments. However, this energy and frequency processing could be affected by other factors, such as fatigue, motivation, expectancy, or irregularity of the background activity at the superior colliculus, thalamic, and other cortical levels (Manjarrez et al., 2007). This would explain the differences among subjects, and this possibility requires further investigation. In summary, these results suggest a general brain dynamics that exhibits deterministically or stochastically induced resonances, as illustrated in Figure 8.

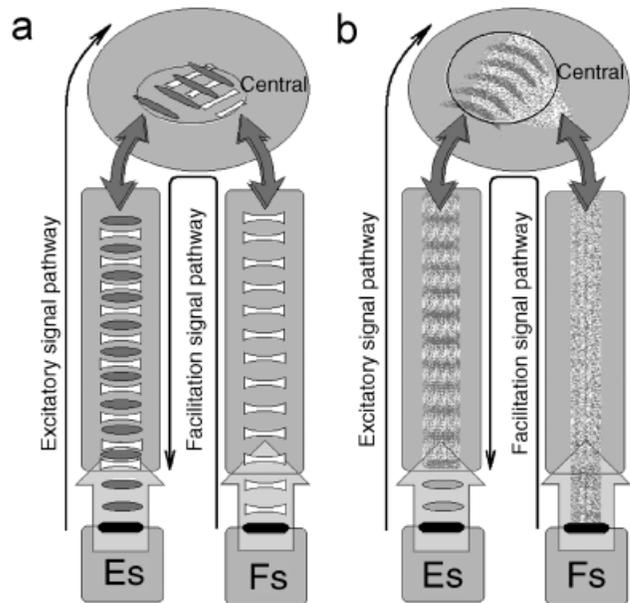


Fig. 8. A graphic rendition demonstrating how peripheral detectors may be influenced by central activity through general multisensory integration. In the case of a deterministic facilitation signal (a), an excitatory signal (convex shape) originates at Es and enters the sensory system from the periphery; the signal cannot be detected at a central level. Simultaneously, the facilitation signal (concave shape) originates at Fs; this signal can be detected at a central level and then goes back to the periphery again (using the excitatory pathway). There, energy transfer takes place, and the excitatory signal can be detected somewhere in the central system. A similar process takes place in the case of a stochastic facilitation signal (b). In this illustration, the convex shapes represent the excitatory signal, and the shading represents the facilitation signal.

In conclusion, the present investigation extends current understanding of MI. Our findings show that certain kinds of MI do not follow the inverse-effectiveness rule, but are consistent with the fact that tactile, visual, and proprioceptive detection and audiovisual comprehension of spoken words are substantially improved at an intermediate level of auditory noise. The notion that a signal applied in another modality could influence peripheral nervous system activity related to tactile stimulation could radically alter current views of the interaction between central and peripheral processing, both in MI and, to some extent, in general. Given the experimental protocols we used, it is clear that the observed effects could not have simply been due to a modulation in attention, arousal, or some form of anticipated motor response. Thus, we can conclude that these transitions in tactile perception come from the way the brain processes the energy and the frequency content of noise and signal.

To explain these MI interactions, we propose a theoretical framework based on physics dynamics. This framework can be summarized as follows: A subthreshold excitatory signal (entering in one sense) that is synchronous with a facilitation signal (entering in a different sense) can be increased (up to a resonant-like level) and then decreased as a function of the content of the facilitation signal, and these dynamics are governed in part by the energy and frequency content of the facilitation signal.

Finally, our results suggest exciting new research directions. For instance, can this or an extended theoretical framework unify the results that follow the inverse-effectiveness rule with the ones discussed here? Within what range of physical frequencies is each interaction observed? How can these dynamics be represented mathematically? And what neural substrates might explain these interactions?

Acknowledgments—This work was supported by the Natural Sciences and Engineering Research Council (NSERC)-Essilor Research Chair and by NSERC operating funds. We would like to thank Lawrence M. Ward for helpful comments on the manuscript, Robert Forget for providing the Grass stimulator, and Patrick Perron for technical assistance.

REFERENCES

- Calvert, G.A., Bullmore, E.T., Brammer, M.J., Campbell, R., Williams, S.C., McGuire, P.K., et al. (1997). Activation of auditory cortex during silent lipreading. *Science*, *276*, 593–596.
- Calvert, G.A., Spence, C., & Stein, B.E. (2004). *The handbook of multisensory processes*. Cambridge, MA: MIT Press.
- de Gelder, B. (2000). Neuroscience: More to seeing than meets the eye. *Science*, *289*, 1148–1149.
- Faubert, J., Hahler, E.-M., Doti, R., & Lugo, J.E. (2007). Auditory noise can facilitate low level visual processing. *Journal of Vision*, *7*, Abstract 866a. Available <http://journalofvision.org/7/9/866/>
- Jousmaki, V., & Hari, R. (1998). Parchment-skin illusion: Sound-biased touch. *Current Biology*, *8*, R190.
- Killeen, P.R. (2005). An alternative to null-hypothesis significance tests. *Psychological Science*, *16*, 345–353.
- Lakatos, P., Chen, C.M., O'Connell, M.N., Mills, A., & Schroeder, C.E. (2007). Neuronal oscillations and multisensory interaction in primary auditory cortex. *Neuron*, *53*, 279–292.
- Laurienti, P.J., Burdette, J.H., Maldjian, J.A., & Wallace, M.T. (2006). Enhanced multisensory integration in older adults. *Neurobiology of Aging*, *27*, 1155–1163.
- Lugo, J.E., Doti, R., & Faubert, J. (2008). Ubiquitous crossmodal stochastic resonance in humans: Auditory noise facilitates tactile, visual and proprioceptive sensations. *PLoS ONE*, *3*(8), e2860. Available <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0002860>
- Macaluso, E., Frith, C.D., & Driver, J. (2000). Modulation of human visual cortex by crossmodal spatial attention. *Science*, *289*, 1206–1208.
- Manjarrez, E., Mendez, I., Martinez, L., Flores, A., & Mirasso, C.R. (2007). Effects of auditory noise on the psychophysical detection of visual signals: Cross-modal stochastic resonance. *Neuroscience Letters*, *415*, 231–236.
- McCurk, H., & MacDonald, J. (1976). Hearing lips and seeing voices. *Nature*, *264*, 746–748.
- Ross, L.A., Saint-Amour, D., Leavitt, V.M., Javitt, D.C., & Foxe, J.J. (2007). Do you see what I am saying? Exploring visual enhancement of speech comprehension in noisy environments. *Cerebral Cortex*, *17*, 1147–1153.
- Schurmann, M., Caetano, G., Jousmaki, V., & Hari, R. (2004). Hands help hearing: Facilitatory audiotactile interaction at low sound-intensity levels. *The Journal of the Acoustical Society of America*, *115*, 830–832.
- Simiu, E. (2002). *Chaotic transitions in deterministic and stochastic dynamical systems*. Princeton, NJ: Princeton University Press.
- Stein, B.E., & Meredith, M.A. (1993). *The merging of the senses*. Cambridge, MA: MIT Press.
- Thurlow, W.R., & Rosenthal, T.M. (1976). Further study of existence regions for the “ventriloquism effect.” *Journal of the American Audiology Society*, *1*, 280–286.
- Wallace, M.T., Wilkinson, L.K., & Stein, B.E. (1996). Representation and integration of multiple sensory inputs in primate superior colliculus. *Journal of Neurophysiology*, *76*, 1246–1266.
- Wells, C., Ward, L.M., Chua, R., & Inglis, J.T. (2005). Touch noise increases vibrotactile sensitivity in old and young. *Psychological Science*, *16*, 313–320.

(RECEIVED 5/23/07; REVISION ACCEPTED 1/21/08)