Optimal integration of auditory and vibrotactile information for judgments of temporal order

Ian Ley [1], Patrick Haggard [2, 3] & Kielan Yarrow [1*]

1. Department of Psychology,
City University

2. Institute of Cognitive Neuroscience,
U.C.L.

3. Department of Psychology,
U.C.L.

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* Author for correspondence:

Kielan Yarrow,
Social Science Building,
City University,
Northampton Square,
London EC1V 0HB

Tel: +44 (0)20 7040 8530
Fax: +44 (0)20 7040 8580
Email: kielan.yarrow.1@city.ac.uk

Abstract

Recent research assessing spatial judgments about multisensory stimuli suggests that humans integrate multisensory inputs in a statistically optimal manner, weighting each input by its normalised reciprocal variance. Is integration similarly optimal when humans judge the *temporal* properties of bimodal stimuli? Twenty four participants performed temporal order judgments (TOJs) about two spatially separated stimuli. Stimuli were auditory, vibrotactile, or both. The temporal profiles of vibrotactile stimuli were manipulated, producing three levels of TOJ precision. In bimodal conditions, the asynchrony between the two unimodal stimuli comprising a bimodal stimulus was also manipulated to determine the weight given to touch. Unimodal data were used to predict bimodal performance on two measures: judgment uncertainty and tactile weight. A model relying exclusively on audition was rejected based on both measures. A second model selecting the best input on each trial did not predict the reduced judgment uncertainty observed in bimodal trials. Only the optimal maximum-likelihood-estimation model predicted both judgment uncertainties and weights, extending its validity to TOJs. We discuss alternatives for modelling the process of event sequencing based on integrated multisensory inputs.

Keywords

Multisensory integration, temporal order judgment, audition, touch, statistical optimality

Introduction

Integrating cues for sensory judgments

In daily life we are often confronted with multiple redundant forms of sensory information which can inform a single perceptual decision. Perhaps the best known example comes from the common situation in which different sensory modalities, such as vision and audition, both provide information about some property of an object, for example the location of a loudspeaker. The observer may use one or more sensory channels to determine where the loudspeaker is, and the question arises as to how information from different modalities is combined or disregarded in order to form a single fused percept (Ernst & Bülthoff, 2004).

In the natural environment, all sensory modalities that provide relevant information for a particular decision tend to be consistent, i.e. each modality specifies the same (true) value for the property that is being judged (although resulting estimates may differ as a result of sensory noise; see later). Under these circumstances, it may be difficult to isolate the contribution of each modality to the final judgment. A common experimental approach has therefore been to introduce a disparity between two sensory inputs (usually without alerting participants to this fact) and require a judgment about the combined percept. In this way it is possible to dissect the influence of each input, by determining how closely the percept follows one input relative to another. For example, Rock and Victor (1964) used a distorting lens to introduce a discrepancy between the seen and felt shape of objects. Their participants reported shapes more consistent with the

visual than with the haptic stimulus. This finding was interpreted as showing total visual dominance, although some influence of the haptic stimulus could still in fact be discerned (Ernst & Bülthoff, 2004). With this finding in mind, it makes sense to talk in terms of the relative weight given to each sensory input, rather than complete reliance on just one source. Another well-studied example where a sensory discrepancy may go unnoticed is the ventriloquist illusion, in which the ventriloquist's speech appears to come from the mouth of their puppet (Müller, 1838, cited in Bertelson & de Gelder, 2004). In laboratory situations, auditory stimuli are generally mislocalised towards synchronised visual stimuli, with a much smaller influence of auditory stimuli on visual spatial localisation (Bertelson & Radeau, 1981; Pick, Warren & Hay, 1969; but see Alais & Burr, 2004).

While data from experiments investigating spatial judgments have tended to indicate that vision is weighted more heavily than either audition or haptics in bimodal judgments, this finding does not necessarily generalise to other kinds of judgments. For example, when participants are required to judge the temporal properties of a bimodal stimulus, audition is often found to dominate over vision and touch. Two examples will serve to illustrate this point.

Firstly, Shams, Kamitani and Shimojo (2000, 2002) presented subjects with a single brief visual stimulus accompanied by one or more brief auditory stimuli, and found that multiple sounds induced subjects to report seeing multiple illusory flashes. A similar phenomenon is evident in the tendencies to both perceive the rate of a rapidly fluttering bimodal rhythmic stimulus to be that of the auditory, rather than the visual, component (Recanzone, 2003; Welch, DuttonHurt & Warren, 1986) and to misperceive the number

of taps to the skin in line with the number of accompanying auditory beeps (Bresciani et al., 2005).

Secondly, Morein-Zamir, Soto-Faraco and Kingstone (2003) building on work by Scheier, Nijhawan and Shimojo (1999) had participants perform a temporal order judgment task, determining which of two near-synchronous lights occurred first. When two task-irrelevant sounds were presented, the first one coming just before the first light and the second one coming just after the second light, performance in the temporal order judgment task improved. This "temporal ventriloquism" has been interpreted as a tendency for each sound to attract the temporally closest light, thus increasing the perceived separation between the two lights (although the second sound appears to be a far more powerful attracter; Morein-Zamir et al., 2003).

The classical literature on multisensory integration has given rise to a well-developed theoretical framework for predicting integration effects. One key concept is that the more appropriate a sensory modality is for the particular judgment that is to be made, the more weight that modality receives when reaching the judgment (Welch & Warren, 1980). To avoid circular reasoning, appropriateness must be measured independently from the bimodal situation. Most explanations refer to the unimodal acuity or precision for the perceptual property that is being assessed (e.g. Welch et al., 1979; see Welch & Warren, 1980, for a review of the early literature). This is entirely in accord with the previously reviewed studies showing a visual advantage for spatial judgments and an auditory advantage for temporal judgments. Although comparisons are complicated by the differences between stimuli used in different sensory modalities, the visual system generally displays excellent spatial acuity, but exhibits low-pass temporal

filtering characteristics that may eliminate fine temporal detail (e.g. Hawken, Shapley & Grosof, 1996). Audition shows the opposite pattern, with tactile acuity falling between these two extremes. Compare for example the threshold for detecting a high-amplitude sinusoidal modulation of light intensity (around 50 Hz , e.g. de Lange, 1958) with the thresholds for detecting such modulation for broadband vibrotactile or auditory noise, lying at around 300 and 1000 Hz respectively (Viemeister, 1979; Weisenberger, 1986).

Statistical optimality and cue integration

Psychological concepts such as modality appropriateness and precision may be difficult to assess in a mathematically rigorous manner. Recently, a number of researchers have attempted to formally describe the manner in which different inputs are weighted and combined for sensory judgments (Ernst & Bülthoff, 2004). A statistical framework has been used in order to define the optimal method for combining inputs (with optimality defined in terms maximising precision) and psychophysical performance has been compared to this prediction. It is assumed that sensory inputs will contain varying degrees of environmental noise, and will be further contaminated by noise during sensory transduction and transmission. Hence the brain is faced with noisy information, and will produce sensory estimates about the state of the environment that vary from trial to trial. In general, any sensory estimate that is not subject to systematic bias will be correct on average, but display variance. Under these conditions, with the assumption of independent Gaussian noise, formal analysis shows that the combined sensory estimate ($\hat{S}$) is best (i.e. has the lowest variance) when all sensory estimates ($\hat{S}_i$, with the subscript

referring to the sensory modality) are combined in a weighted average (Equation 1). The weight given to a specific estimate (w_i) should be inversely proportional to the variance of that sensory estimate (σ^2_j, Equation 2).

$$\hat{S} = \sum_i w_i \hat{S}_i \quad \text{with } \sum_i w_i = 1 \qquad (1)$$

$$w_j = \frac{1/\sigma_j^2}{\sum_i 1/\sigma_i^2} \qquad (2)$$

Individual sensory variability can be estimated directly by recording estimates across a number of trials in unimodal conditions. If we concentrate on the bimodal case, for example combining an auditory stimulus with variance σ^2_A and a tactile stimulus with variance σ^2_T, we can re-write Equation 2 as follows:

$$w_T = \frac{1/\sigma_T^2}{\left(1/\sigma_T^2\right) + \left(1/\sigma_A^2\right)} = \sigma^2_A / (\sigma^2_A + \sigma^2_T) \qquad (3)$$

Where the optimal weighting rule is followed, variability in the multimodal case will always be lower than the variability in the best of the contributing unimodal sensory estimates. The bimodal variance σ^2_{AB} can be determined from Equation 4:

$$\sigma^2_{TA} = \sigma^2_A \sigma^2_T / (\sigma^2_A + \sigma^2_T) \leq \min(\sigma^2_A, \sigma^2_T) \qquad (4)$$

Experiments can be devised which test how closely human judgments conform to the predictions of such an optimal maximum likelihood estimation (MLE) model. Conformity would suggest that the dominance of one sensory modality for any particular judgment does not imply an inflexible reliance on that modality for all judgments of a particular type (e.g. spatial, temporal) but rather a tendency to favour more precise inputs over less precise inputs, regardless of their sensory origin. Examples of this approach include the work of Hillis, Watt, Landy and Banks (2004) for the combination of depth cues, Van Beers, Sittig and Gon (1999) for combining visual and proprioceptive information in two dimensions to estimate the position of an unseen arm, Heron, Whitaker and McGraw (2004) for estimating the effect of a transitory auditory stimulus on the perceived position of reversal of a moving visual stimulus, and Shams, Ma and Beierholm (2005) for assessing the impact of transient beeps on the perceived number of transient flashes and vice versa. The current research was influenced heavily by the experimental design used by Ernst and Banks (2002) so that study will be described in more detail as a concrete example.

Ernst and Banks (2002) used two force-feedback devices attached to the forefinger and thumb to create virtual haptic objects (raised horizontal bars). Spatially compatible visual stimuli were created using random dot stereograms. In unimodal conditions, participants had to compare a stimulus of standard (55 mm) height with a comparison stimulus that varied in height about this standard value. Noise could be added to the visual stimulus in order to vary the difficulty of the discrimination. Variance was estimated as the squared width of the psychometric function fitted to a participant's responses. Stimuli were designed so that the haptic stimulus variance fell within the range

of variances for the visual stimuli. In bimodal conditions, the different visual stimuli were combined with the haptic stimulus in the same judgment. A further manipulation varied each component of the bimodal standard, so that it averaged 55 mm but might for example be composed of a shorter visual stimulus and a longer haptic stimulus. This allowed the authors to determine the weight given to each modality by determining the change in the point of subjective equality produced by a particular visual-haptic discrepancy. Ernst and Banks (2002) found that the variances and weights determined from the bimodal condition were in close agreement with the optimal MLE model described above. Visual weights decreased as the visual stimulus became noisier, and bimodal variance was always lower than the better of the two contributing unimodal variances. A very similar approach was used by Alais and Burr (2004), who varied the spatial precision of a visual stimulus to show that the ventriloquist effect also represented an example of statistically optimal integration.

Rationale for the current investigation assessing temporal order judgments

To date, those multisensory studies that have tested the optimal integration model have assessed mainly spatial judgments, where vision would traditionally be assumed to dominate. More recently, studies have begun to assess judgments which may depend partially upon temporal acuity, such as counting the number of rapid transient events in a short train (Bresciani, Dammeier & Ernst, 2006; Bresciani & Ernst, 2007; Shams et al., 2005; Wozny, Beierholm & Shams, 2008) or comparing the rate of a flickering or fluttering stimulus (Roach, Heron & McGraw, 2006; Wada, Kitagawa & Noguchi, 2003).

These studies have generally supported the MLE model, albeit with the addition of model parameters intended to downplay integration in the context of obvious sensory discrepancies. However, tasks like these do not really investigate timing mechanisms, but rather mechanisms of numerosity coding and rate perception. In the current study, we wished to assess whether judgments about the *sequencing* of events in time would also exhibit statistically optimal multisensory integration. For example, when we witness a car crash and must place it in temporal context, do we perceive the time of collision based on either visual or auditory information, or combine both in an optimal manner? To this end, we developed a temporal order judgment (TOJ) task in which variability could be manipulated in a manner analogous to the changes in visual noise introduced by Ernst and Banks (2002).

In TOJ tasks, subjects are presented with two brief stimuli in rapid temporal succession and asked to discriminate which came first. The method has been widely used throughout the history of experimental psychology (Spence, Shore & Klein, 2001). It provides the most direct way to assess how events are ordered to construct a subjective timeline. Studies investigating temporal ventriloquism indicate that multisensory integration can be assessed using TOJs (Morein-Zamir et al., 2003; Scheier et al., 1999). Furthermore, irrelevant stimuli in a second modality that are presented in either identical or opposite order to the attended stimuli in a TOJ task have been shown to affect judgements of temporal order (Kitazawa et al., 2007; Sherrick, 1976). However, we are not aware of any previous attempt to compare precisely the TOJs made in a bisensory task with predictions based on Bayesian models. Given the precision of these models, this represents an important gap in our knowledge. To investigate the issue, we presented

vibrotactile and auditory stimuli, presented on the left and right sides, in unisensory and bisensory conditions, whilst manipulating the difficulty of the vibrotactile judgment. On some bisensory trials, we introduced a very small asynchrony between the auditory and vibrotactile components of the right hand stimulus. Our subjects judged the side from which the first stimulus came. In this way we were able to generate an experimental situation that promoted optimal integration, and to accurately test the optimal MLE model against judgments of temporal order.

In order to evaluate the MLE model, our approach was to generate predictions from three models, and attempt to demonstrate statistically significant mean deviations from two of the three in order to demonstrate the plausibility of the remaining model. We also compared the models directly on their squared errors of prediction. The first model assumed that because audition has generally been found to dominate over vision and touch for temporal judgments, subjects would simply rely on the auditory information and ignore the vibrotactile information. We refer to this as the *rely on audition* model. The second model assumed that subjects would use only one sensory modality on each trial, but that they would flexibly select the sensory modality depending on which modality contained the stimulus which provided the most precise information about temporal order. We refer to this as the *best sensory estimate* model. Finally, the third model assumed statistically optimal bisensory integration, and is referred to as the *maximum likelihood estimation (MLE)* model.

Method

Subjects

Initially, 24 participants were tested. Based on this data set it was impossible to discriminate the MLE model from the best sensory estimate model, with neither being statistically distinguishable from the data. In order to better discriminate between models, we decided to reject and replace a subset of outlying subjects to make our sample more homogeneous. Subjects who returned any point of subjective simultaneity or judgment uncertainty estimate (see analysis, below) that deviated by more than four standard deviations from the group mean in one or more of the 13 unimodal and bimodal conditions were excluded. This led to the rejection of four subjects, who were then replaced to yield a final sample of 24 participants (13 male, mean age = 25.6, SD = 3.9).

Apparatus and stimuli

The experiment was controlled by a PC producing auditory and vibrotactile stimuli at 44100 Hz using a 12 bit A/D card (National Instruments DAQCard 6715). We confirmed the correct timing of output signals using a 20 MHz storage oscilloscope (Gould DSO 1604). Both auditory and vibrotactile stimuli were Gaussian-windowed 120 Hz sinusoids. The Gaussian windowing procedure was used to produce stimuli that could be temporally smeared to varying extents; a small standard deviation produced a brief, sharply defined stimulus whereas a large standard deviation produced a longer stimulus with an indistinct peak. In addition to varying the standard deviation of the window, we also varied its peak intensity. The area under the Gaussian window was held constant,

such that a stimulus with a small standard deviation had a high peak intensity and vice versa. The resulting windowed sinusoids were then embedded in low-frequency background noise. A one second segment of white noise was produced by generating random voltages from a uniform distribution. This signal was digitally filtered with a second order bidirectional Butterworth filter with a high cut frequency of 240 Hz. Windowed sinusoids were added to low-pass noise to produce our final stimuli. We used three vibrotactile stimuli and one auditory stimulus, with parameters selected based on pilot work, and modified slightly after the first eight subjects had been analysed. For the first eight subjects, the auditory stimulus has a maximum peak-to-peak voltage of 4.0 V and a standard deviation of 59 ms, and was embedded in filtered noise with an RMS voltage of 0.785 V. The three vibrotactile stimuli had maximum peak-to-peak voltages of 4.0, 8.0 and 17.1 V, with standard deviations of 59, 29 and 13 ms respectively. They were embedded in filtered noise with an RMS voltage of 0.392 V. For the remaining subjects, the auditory stimulus was adjusted to have a maximum peak-to-peak voltage of 6.5 V and a standard deviation of 36 ms, while the intermediate vibrotactile stimulus was also adjusted to have a peak-to-peak voltage of 6.5 V and a standard deviation of 36 ms. Background filtered noise was unchanged, being higher in the auditory case. These changes were made in order to provide a better match between the intermediate vibrotactile stimulus and the auditory stimulus (and also a greater difference between these stimuli and the two extreme vibrotactile stimuli), which maximises the difference in model predictions (see below). The stimuli used for the first eight subjects are shown in Figure 1 part A. Note that these are the voltages sent to the vibrotactile and auditory actuators, not necessarily the physical stimuli that where produced by these components.

Subjects sat with their head on a chin rest, having adjusted its height to suit their preferred posture. Auditory stimuli were presented from two small speakers, located below and in front of the subject's head on a desk top, one to the left and one to the right. The distance between the speakers was 30 cm. They were 20 cm in front of the head rest. Their distance below ear level varied from subject to subject, but was typically around 40 cm. Vibrotactile stimuli were delivered via two small (1 cm diameter) ceramic piezoelectric disks coated in plastic. The disks were driven from a custom-built amplifier, and did not produce audible noises with any of the stimuli we used. They were attached to the underside of the desk in front of the subject, with one disk mounted directly below each auditory speaker. The disks were gripped comfortably between index finger and thumb.

INSERT FIGURE 1 AROUND HERE

Design

The experiment consisted of two phases: a unimodal phase, in which baseline auditory and vibrotactile performance was assessed separately, and a bimodal phase in which combined auditory/vibrotactile stimuli were presented. The order of the two phases was counterbalanced across subjects. In the unimodal phase, subjects received one block of 75 trials with auditory stimuli and one block of 225 trials with vibrotactile stimuli. The auditory block contained a single kind of stimulus. The vibrotactile block contained 75 trials with each of the three types of vibrotactile stimulus, in a pseudorandom order. The

order in which the two unimodal blocks that made up the unimodal phase were received was counterbalanced across subjects.

In the bimodal phase, subjects received a single block of 675 trials. A two factor (3x3) design was used. The first factor, *tactile difficulty,* varied the parameters of the tactile stimulus as discussed above. The second factor, *auditory-tactile disparity,* varied the temporal position of the peak of the right-sided vibrotactile stimulus relative to the peak of the right-sided auditory stimulus. The peaks of the two left-sided stimuli always coincided exactly. Hence on each trial the auditory stimulus was combined with one of three tactile stimuli, with the right-sided tactile stimulus presented at one of three temporal offsets relative to the right-sided auditory stimulus (-25 ms, 0 ms and 25 ms). An example of one trial from the bimodal phase of the experiment is shown in Figure 1 part B. Subjects received 75 trials from each condition in a pseudorandom order.

Procedure

In the unimodal phase, one stimulus was delivered to the right side and one to the left side on each trial. Both stimuli came from the same modality and were generated using the same Gaussian window (i.e. had the same temporal smear and peak intensity). The noise components of each of the two one-second long stimuli were completely identical, and began and finished at the same time. In contrast, the windowed sinusoidal components of the two stimuli could be temporally offset from one another. The Gaussian window for the right-sided stimulus peaked at 500 ms, exactly half way into the stimulus. The Gaussian window for the left-sided stimulus could peak anywhere from

300 ms before the right-sided stimulus to 300 ms after the right-sided stimulus. Participants judged whether the left or the right stimulus had occurred first, having been directed to attend to the distinct sinusoidal peaks, not the onset of the background noise. Their responses were entered into the computer by the experimenter.

The delay between the right and left-sided stimuli varied from trial to trial. It was selected randomly on each trial from a condition-specific distribution. There was a single distribution for the auditory block and separate ones for each of the three stimuli used in the vibrotactile block. Each distribution was initially uniform, containing delay values from -140 to +140 ms in 20 ms increments, but was updated after each accepted trial according to the generalized P'olya urn model (Rosenberger & Grill, 1997; k = 8). Distributions could therefore expand to include delay values from -300 to +300 ms. This procedure produces many values close to the point of subjective simultaneity.

In the bimodal phase, the procedure was similar, but four stimuli, two vibrotactile and two auditory, were delivered on each trial. Subjects were told that the two stimuli on the left would peak at the same time, as would the two stimuli on the right, and were required to judge which of the two combined (bimodal) stimuli came first. In fact, while the peaks of the two stimuli on the left were indeed synchronous, the peaks of the two stimuli on the right could either also be synchronous, or the vibrotactile component could be offset slightly from the auditory component by 25 ms in either direction. The auditory component of the right-sided stimulus peaked at 500 ms. The vibrotactile component of the right sided stimulus peaked at 475, 500, or 525 ms. The two left-sided stimuli peaked with a delay of -300 to +300 ms, determined relative to the auditory component of the right-sided stimulus. Separate adaptive distributions were maintained to randomly select

delays in each of the nine conditions (three levels of tactile difficulty crossed with three levels of right-sided auditory-tactile disparity).

Analysis

The proportion of times that a subject judged the right-sided stimulus to have occurred first for each delay value that had been presented was determined separately in each condition. Cumulative Gaussian psychometric functions were fitted to these data using the psignifit toolbox version 2.5.6 for Matlab (see http://bootstrap-software.org/psignifit/) which implements the maximum-likelihood method described by Wichmann & Hill (2001). Points of subjective simultaneity (PSSs) and judgment uncertainty were estimated from these functions. The PSS was estimated from the delay value where the "right first" judgment occurred with a probability of 0.5. Judgment uncertainty is a threshold value similar to the commonly assessed just-noticeable difference (JND), and was estimated as the difference between the delay values that yielded "right first" judgments with probabilities of 0.5 and 0.84.

The bimodal conditions were used to determine the manner in which participants combined information from the tactile and auditory modalities to reach a temporal judgment. We wished to assess both the bimodal judgment uncertainty, and the weight given to the tactile modality, for the combination of the auditory stimulus with each of the three different vibrotactile stimuli. To determine the bimodal judgment uncertainty, we averaged the judgment uncertainty values estimated for the three bimodal conditions sharing a particular tactile stimulus (e.g. the -25, 0 and +25 ms disparity conditions with

the tactile stimulus of gradual temporal profile) as the manipulation of auditory-tactile asynchrony for the right hand stimulus would not be expected to change the slope of the psychometric function given the range of stimuli we used. To determine the weight given to the tactile modality, we determined the difference between the PSSs estimated for the +25 and -25 ms disparity conditions. To normalise this value, we divided it by 50, because 50 is the expected change in PSS if subjects had based their judgments entirely on the tactile modality.

Data from the three unimodal conditions were used to predict performance in the bimodal condition under each of the three models considered in the introduction. For the rely on audition model, predicted judgment uncertainty in each of the three bimodal cases was equal to judgment uncertainty in the unimodal auditory condition, while the predicted tactile weights were all zero. For the best sensory estimate model, the predicted judgment uncertainty was taken as the lower of the unimodal auditory or the unimodal tactile judgment uncertainties for the relevant tactile stimulus profile. Predicted tactile weights were set to zero if the auditory judgment uncertainty was lower than the relevant tactile judgment uncertainty, and to 1.0 if the opposite was the case. Finally, for the MLE model, predicted judgment uncertainties and tactile weights were determined according to equations 4 and 3 in the introduction respectively.

Traditional measures of goodness of fit were not appropriate to test our models, because we were not fitting models with free parameters to a data set, but rather testing the predictions of each model on a new data set. The predictions from each of the three models were therefore compared to the values estimated directly from the bimodal conditions. Predictions were also used to produce an additional measure of predictive

success: mean squared deviation. All comparisons were made using standard parametric statistics (ANOVAs with Greenhouse-Geisser corrections for violations of sphericity and repeated measures t-tests).

Results

INSERT FIGURE 2 AROUND HERE

Unimodal Data

Figure 2 shows the results of the four unimodal conditions in which subjects performed temporal order judgments between two lateralised stimuli, both coming from the same sensory modality. A single auditory stimulus was assessed, along with three vibrotactile stimuli constructed so as to vary the difficulty of this temporal discrimination. Figure 2 part A illustrates how judgment uncertainty was determined. To produce this figure, the data from all 24 participants were combined in each unimodal condition, and fitted with a cumulative Gaussian sigmoid function. The slopes of the fitted sigmoids reflect the difficulty of each judgment, with steep slopes indicating less noisy judgments. Figure 2 part B shows the mean judgment uncertainty in each condition determined from our actual analysis. To generate these data we fitted a different sigmoid to each individual participant's data in each condition, calculated judgment uncertainty, and then averaged across the group. Hence judgment uncertainties differ somewhat from those that would be estimated from the fits shown in part A. Figure 2 part B indicates that

our manipulation of difficulty in the vibrotactile conditions was successful. The tactile stimulus with the gradual temporal profile yielded the highest judgment uncertainty, considerably higher than that of the auditory condition, while the steeply profiled tactile condition yielded the lowest judgment uncertainty, lower than that of the auditory condition. The intermediate tactile condition was intermediate in difficulty between these extremes and showed similar, but slightly lower judgment uncertainty compared to the auditory condition. Although our measure of judgment uncertainty is somewhat unusual, being the difference between the mid point of the psychometric function and the 0.84 point (one standard deviation along the cumulative Gaussian), the judgment uncertainties can be easily converted to just noticeable differences (JNDs; the difference between the 0.75 and 0.5 points) to facilitate comparison with other studies. The JND is 0.67 times the judgment uncertainty value we report; for the unimodal data, JNDs therefore ranged from 214 ms (for the gradual tactile stimulus) to 68 ms (for the steep tactile stimulus).

The range of uncertainties in our data is not quite as great as would have been ideal, but differences across tactile conditions were statistically reliable as assessed with a one-way repeated measures ANOVA ($f = 8.31$, corrected $df = 1.24, 28.43$, $p = 0.005$) and indicate that our experimental manipulations were suitable to provide a test of our three models using data collected in bimodal conditions.

INSERT FIGURE 3 AROUND HERE

Bimodal Data: Judgment Uncertainty

In addition to the unimodal conditions, each participant discriminated the temporal order of combined bimodal stimuli presented to the left and right. To produce these bimodal stimuli, the auditory stimulus could be combined with each of the three vibrotactile stimuli. Figure 3 part A illustrates how judgment uncertainty was determined. The combined data across all 24 participants is displayed for the three conditions which combined the auditory stimulus with each of the vibrotactile stimuli without introducing any between-modality asynchrony. The best fitting sigmoids are also shown.

For our actual analysis, we fitted each participant's data in each condition with a separate sigmoid to determine judgment uncertainty. We then produced a single estimate of judgment uncertainty for each participant and each combination of the auditory stimulus with one of the three vibrotactile stimuli. To do this, we averaged across the three conditions that introduced a slight between-modality asynchrony, as any differences between these would only be relevant for assessing weights (see below). In addition, we used each participant's judgment uncertainties in the unimodal conditions to predict their bimodal scores based on three possible models: The rely on audition model, which assumes that the vibrotactile input is disregarded; the best sensory estimate model, which assumes that on each trial the more precise modality is used; and the MLE model, which combines the two inputs weighted according to their precision. Figure 3 part B shows the mean judgment uncertainty averaged across all participants, along with the mean predicted judgment uncertainty for each of the three models. These judgment uncertainties equate to JNDs of 79, 58 and 53 ms for the gradual, intermediate and steep conditions respectively.

The pattern of mean judgment uncertainties supports the MLE model. When the vibrotactile component of the bimodal stimulus had a gradual or intermediate temporal profile, performance was almost identical to the MLE prediction and better than either the rely on audition or best sensory estimate predictions. For the steep vibrotactile stimulus, MLE and best sensory estimate predictions were very close to one another, and actual performance was about mid-way between these two predictions.

INSERT TABLE 1 AROUND HERE

A comparison of the bimodal judgment uncertainties with the predictions of each model, like that shown in Figure 3b, allows us to visualise the difference between the model's predictions and the mean of the data. It is possible, however, for a model to achieve a good prediction in terms of the mean deviation, but be relatively poor at predicting the data of each individual participant (so long as the different errors of prediction for each subject sum to around zero). For this reason, we also calculated the mean squared deviation of each model from the bimodal data, to measure variation in the model's predictive success. These data are shown in Table 1. Table 1 conforms broadly with Figure 3b, and shows that the MLE model had the lowest mean squared error for all three tactile profiles.

To investigate the predictive power of each model statistically, we first carried out a series of two-way (2x3) repeated-measures ANOVAs to assess mean deviations of model predictions from the bimodal data. Each ANOVA compared one model's predictions with the empirical data (the factor *model*) at each level of vibrotactile

stimulus temporal profile (the factor *tactile profile*). Comparing empirical data with the rely on audition model, the ANOVA revealed a main effect of model ($f = 12.76$, $df = 1, 23$, $p = 0.002$), a main effect of tactile profile ($f = 10.42$, corrected $df = 1.19, 27.43$, $p = 0.002$) and an interaction ($f = 10.42$, corrected $df = 1.19, 27.43$, $p = 0.002$). The main effect of model allows us to reject this model as a viable explanation of bisensory performance in our task. The interaction shows that this rejection is most compelling when the vibrotactile stimulus had a steeper profile.

Comparing the data with the best sensory estimate model revealed a main effect of model ($f = 4.30$, $df = 1, 23$, $p = 0.049$) and a main effect of tactile profile ($f = 10.56$, corrected $df = 1.28, 29.34$, $p = 0.002$) with no interaction ($f = 1.30$, corrected $df = 1.73, 39.85$, $p = 0.280$). Once again, the main effect of model allows us to reject this explanation.

In contrast to the findings for the first two models, comparing empirical data with the MLE model revealed a main effect of tactile profile ($f = 11.36$, corrected $df = 1.19, 27.45$, $p = 0.001$) but no main effect of model ($f = 0.003$, $df = 1, 23$, $p = 0.956$) and no interaction ($f = 0.62$, corrected $df = 1.73, 39.76$, $p = 0.521$). Of the models we investigated, only this one cannot be rejected based on observed judgment uncertainties in bimodal conditions.

A supplementary analysis was carried out on the mean squared deviations for each model. A two-way (3x3) repeated measures ANOVA compared mean-squared deviations of bimodal judgment uncertainty data from model predictions, with the factor *model* comparing the three models, and the factor *tactile profile* comparing the three different vibrotactile stimulus profiles. There was a main effect of model ($f = 4.85$,

correct df = 1.01, 23.12, p = 0.038) but no main effect of tactile profile (f = 2.56, corrected df = 1.09, 24.97, p = 0.12) and no interaction (f = 3.08, corrected df = 1.08, 24.86. p = 0.089). Pairwise follow ups (Tukey's LSD) investigating the main effect of model collapsed across the three levels of tactile profile showed significant differences between all three models, with the MLE model having a significantly lower mean squared deviation than either the best sensory estimate model (p = 0.025) or the rely on audition model (p = 0.035), and the best sensory estimate model having a significantly lower mean squared deviation than the rely on audition model (p = 0.042).

During testing, we rejected and replaced four subjects in order to homogenise our sample and increase the likelihood of being able to discriminate statistically between them. This change was intended to be neutral with regard to the proportion of subjects appearing to provide support for each model. If a model is accurate, we would expect approximately half of the subjects to yield bimodal estimates above model predictions, and half of the subjects to yield estimates below model predictions. In the initial sample, the proportion of subjects scoring below the predictions of the MLE model was 11/24 in the gradual tactile condition, 10/24 in the intermediate condition, and 13/24 in the steep condition. For the final sample, these proportions changed only slightly, to 11/24, 12/24 and 12/24 respectively. Proportions scoring below the predictions of the best sensory estimate model in the initial sample were 15/24, 16/24 and 17/24, changing to 16/24, 17/24 and 17/24 for the final sample. Finally, for the rely on audition model, initial proportions scoring below predictions were 17/24, 19/24 and 21/24, with proportions in the final sample being 18/24, 20/24 and 22/24 respectively. Model predictions and data

are shown for each participant separately in the appendix, along with 95% confidence intervals.

INSERT FIGURES 4 & 5 AROUND HERE

Bimodal Data: Vibrotactile Weights

In bimodal conditions, the relationship between the two unimodal stimuli that made up the bimodal stimulus on the right hand side was manipulated in a subtle manner. The vibrotactile component could be synchronous with the auditory component, or either precede or follow it by 25 ms. Participants were not alerted to this manipulation (they were told that the two components would always be synchronised) and only one participant spontaneously asked about such a manipulation. On further discussion it transpired that this question had been motivated by his expert understanding of multisensory research methodologies rather than any perceived asynchrony.

Figure 4 illustrates how changes in points of subjective simultaneity (PSSs) were used to determine the weight given to the vibrotactile modality for each bimodal combination of the auditory and one of the three vibrotactile stimuli. Data is shown for all 24 participants in the three bimodal conditions in which the auditory stimulus was combined with the steeply profiled vibrotactile stimulus. Best fitting sigmoids are displayed for conditions in which the right hand bimodal stimulus included a small (25 ms) asynchrony between auditory and vibrotactile components, or no such asynchrony.

The curves are clearly shifted along the horizontal axis, indicating that the change in the relative timing of the vibrotactile stimulus influenced participant's PSSs.

For our actual analysis, we fitted each participant's data with a separate sigmoid in each bimodal condition and determined the PSS. The change in PSS between the -25 ms and +25 ms asynchrony conditions for a particular vibrotactile profile was used to determine the weight given to that vibrotactile stimulus. We also used the judgment uncertainties estimated for each subject in unimodal conditions to form predictions about vibrotactile weights based on our three models (rely on audition, best sensory estimate and MLE). Figure 5 shows mean vibrotactile weights across participants based on bimodal data, along with mean predictions for the three models.

The pattern of vibrotactile weights is not entirely consistent with any of the three models. It is closer to the predictions of the best sensory estimate and MLE models, which both predict that weights should rise as vibrotactile strength increases, than the rely on audition model, which does not, but the slight drop from the medium to high strength conditions is not predicted by any model. However, the large error bars suggest a cautious interpretation. Overall, means are closest to the predictions of the MLE model.

INSERT TABLE 2 AROUND HERE

As with the judgment uncertainty data, we also determined mean squared deviations as an additional measure of each model's predictive success. Mean squared deviations are shown in Table 2. In general, the MLE model produced considerably lower mean squared deviations than the rely on audition model, and slightly lower values than

the best sensory estimate model, although the best sensory estimate model was most successful for the gradual tactile condition.

To investigate the predictive power of each model statistically, we first carried out three two-way (2x3) repeated-measures ANOVAs to assess mean deviations of each model's tactile weight predictions from the weights estimated using the bimodal data. Each ANOVA compared one model's predictions with the empirical data (the factor *model*) at each level of vibrotactile stimulus temporal profile (the factor *tactile profile*).

Comparing empirical data with the rely on audition data, there was a main effect of model ($f = 32.68$, $df = 1, 23$, $p < 0.001$) but no main effect of tactile profile ($f = 0.98$, corrected $df = 1.57, 36.18$, $p = 0.367$) and no interaction ($f = 0.98$, corrected $df = 1.57, 36.18$, $p = 0.367$). The main effect of model allows us to reject this model as an explanation of bisensory performance in our TOJ task. However, comparing empirical data with the best sensory estimate and MLE models we were unable to reject either model. In both cases there was a main effect of tactile profile (best sensory estimate: $f = 4.61$, corrected $df = 1.52, 35.04$, $p = 0.025$; MLE: $f = 3.63$, corrected $df = 1.48, 34.01$, $p = 0.05$) but no main effect of model (best sensory estimate: $f = 0.45$, $df = 1, 23$, $p = 0.507$; MLE: $f = 0.11$, $df = 1, 23$, $p = 0.740$) and no interaction (best sensory estimate: $f = 1.38$, corrected $df = 1.89, 43.37$, $p = 0.262$; MLE: $f = 0.69$, corrected $df = 1.72, 39.47$, $p = 0.485$).

A supplementary analysis was carried out on the mean squared deviations for each model. A two-way (3x3) repeated measures ANOVA compared mean-squared deviations of bimodal tactile weight estimates from model predictions, comparing across the three models, and also the three different vibrotactile stimulus profiles. There was a

main effect of model ($f = 5.79$, correct df = 1.07, 24.69, $p = 0.022$) but no main effect of tactile profile ($f = 2.01$, corrected df = 1.35, 31.03, $p = 0.163$) and no interaction ($f = 0.77$, corrected df = 2.32, 53.35. $p = 0.486$). Pairwise follow ups (Tukey's LSD) investigating the main effect of model collapsed across the three levels of tactile profile showed a significant difference between the MLE model and the rely on audition model ($p = 0.004$) and a marginally significant difference between the best sensory estimate model and the rely on audition model ($p = 0.051$) but no significant difference between the MLE model and the best sensory estimate model ($p = 0.538$). The two analyses of tactile weights therefore yielded similar findings: Participants were clearly making use of the tactile stimulus on some or all trials, but the precise manner in which the auditory and tactile stimuli were used cannot be determined using the weight data alone.

Discussion

Our participants judged the temporal order of auditory and vibrotactile stimuli under both unimodal and bimodal conditions. In bimodal conditions, the influence of the vibrotactile stimulus on the combined judgment was assessed by introducing a small discrepancy between the auditory and vibrotactile components of the right-hand combined stimulus. Participants clearly took account of the vibrotactile stimulus when judging temporal order. Performance under unimodal conditions was used to make predictions about bimodal performance based on three models. For weight data, we were able to reject statistically a model in which subjects relied entirely on audition to perform the bimodal task, but were unable to reject either a strategy that selects the more precise

input on each trial or the MLE model which implies weighted summation of inputs according to their precision. However, when judgment uncertainty was determined in bimodal conditions, we found that subjects consistently performed at a higher level than that achieved in either unimodal condition. Only the MLE model predicts this improved level of judgment uncertainty. Furthermore, we were able to reject statistically both alternative models as explanations of our data.

The findings related to observed bimodal judgment uncertainties are particularly important for the following reason. It is possible to mimic the result predicted by the MLE model for sensory weights by the alternative strategy of using only one modality on each trial, but using each modality on a proportion of trials determined by the precision of that modality in unimodal conditions (Ernst & Bülthoff, 2004). However, this strategy does not predict the increase in precision that is the true hallmark of the MLE model. Thus far, no alternative model has been presented which can predict the low levels of judgment uncertainty observed here, so the MLE model is strongly favoured by our data.

Our study represents a formal test of the MLE model of multisensory integration for judgments of temporal order. To our knowledge, there have been no studies published previously on this specific issue. The MLE model has been shown to account well for the integration of visual and haptic spatial information (Ernst & Banks, 2002) and for the integration of visual and auditory spatial information (Alais & Burr, 2004). Our data conform with findings from previous studies suggesting that audition dominates over vision (Recanzone, 2003; Welch et al., 1986; Morein-Zamir et al., 2003; Scheier et al., 1999; Shams et al., 2000) and touch (Bresciani et al., 2005) for tasks with a temporal component: Because audition would be expected to have high precision in these tasks, the

MLE model can account for its apparent domination, just as it accounts for our audiotactile data. Unlike most previous studies, we provide a very detailed quantitative analysis of bisensory integration when the relative precision of each modality is varied, and show that touch can also be important under the appropriate circumstances (i.e. when it forms the more reliable input). Interestingly, this finding is consistent with an early study showing a reciprocal influence of distracting auditory and tactile stimuli on temporal order judgements made in the other modality (Sherrick, 1976).

It may be objected that the rely on audition model is something of a straw man, as very few previous studies have suggested complete auditory dominance over touch for temporal judgments. However, our second alternative model, the best sensory estimate model, is certainly a realistic contender. Like the MLE model, it implies sophisticated knowledge about the precision of each sensory input. Nonetheless, we were able to reject this model and thus favour the MLE model which suggests that appropriate weighting and combination of information also occurs *on every trial*.

While ours is the first study to demonstrate statistically optimal integration of bisensory inputs for judgments of temporal order, it is not the first to suggest that temporal order judgments may take into account multiple sources of information in a mathematically sophisticated way. For example, prior probability distributions based on previous experience appear to be weighted and integrated with current sensory estimates to perform TOJs (and also anticipate stimulus arrival times) in a Bayesian manner (Miyazaki, Nozaki & Nakajima, 2005; Miyazaki, Yamamoto, Uchida & Kitazawa, 2006). In simple terms, participants expect asynchronies that they have repeatedly experienced (although they may also show additional and alternative recalibration effects; see for

example Fujisaki, Shimojo, Kashino and Nishida, 2004, for audiovisual stimuli, Navarra, Soto-Faraco and Spence, 2007, for audiotactile ones, and Hanson, Heron and Whitaker, 2008, for all bimodal combinations of vision, audition and touch). Expectations based on priors are easily incorporated into an MLE model of multisensory integration under a single Bayesian framework, so it would be interesting to test for such effects in unison (Ernst & Bülthoff, 2004).

Because our interpretation relies heavily on changes in the precision with which subjects performed the TOJ task, it is important to emphasise that practice effects could not have generated our findings. The order in which subjects performed unimodal and bimodal conditions were counterbalanced, so that any improvement (or decrement) over time did not apply to just one phase of the experiment. It might also be objected that we rejected four subjects prior to obtaining our final sample. These subjects were not uniform in terms of the model they best supported, and the motivation for excluding them was the variability they introduced, rather than their conformity to any particular prediction. However, it should be noted that one of these four participants was an extreme outlier, in that his performance was competent in the unimodal conditions, but collapsed almost entirely in the bimodal conditions (which were performed subsequently, i.e. with additional practice). None of our models predicted this pattern, and we wonder whether there was something unusual about this participant that meant an additional redundant stimulus interfered strongly with the first stimulus, rather than being adequately ignored or usefully integrated.

How might our participants have determined the reliability of each input in order to integrate them appropriately? Subjects could not tell in advance of a trial which kind of

tactile stimulus they were to receive. However, they received only four kinds of stimulus during the experiment (one auditory and three vibrotactile) so it is possible that they were able to build up an accurate estimate of the precision of each kind of stimulus over multiple trials, then classify the tactile component of the bimodal stimulus in order to achieve optimal integration. Given, however, that they received no feedback during the experiment, it is unclear how precision could be accurately determined in this manner. We therefore favour the alternative idea that participants were able to flexibly and near instantaneously estimate the precision of each input on each and every trial, i.e. that the noise of a sensory estimate is represented alongside that estimate in a trial by trial manner. This conclusion has been favoured by other researchers following demonstrations of MLE integration where stimuli varied much more widely than was the case here (Hillis et al., 2004).

Turning to possible neurocognitive models for our bimodal TOJ task, it is tempting to infer from these data that tactile and auditory estimates about time of arrival were integrated for each combined stimulus, with these optimally combined stimuli undergoing subsequent comparison to determine their temporal order. This interpretation is intriguing, because it is not immediately obvious how such a process could be accomplished in real time. Sensory inputs will be represented in the brain following a delay reflecting their processing and transmission times. Simple bottom-up models of the TOJ task suggest that separate inputs arrive at some decision centre, where they are compared using a more or less sophisticated decision rule to determine temporal order (Sternberg & Knoll, 1973; Ulrich, 1987). We can also consider how MLE integration might be accomplished in the brain. One scheme for achieving MLE integration suggests

a point by point multiplication of two population representations in which each node corresponds to a particular value, and the degree of activation indicates the strength of evidence for that value (Knill & Pouget, 2004). Noisier inputs yield more distributed population responses. For a TOJ task, the values that are represented by different nodes would need to be estimates of time of arrival, which implies that time is no longer represented as time (i.e. in the timing of neural activity) but rather has been converted into a spatial code. Combined sensory estimates would then be compared to evaluate temporal order. This analysis might lead us to reject a real-time account of TOJ task performance and favour the involvement of higher level, potentially post-hoc interpretative processes (Dennett & Kinsbourne, 1992).

This, however, is not the only plausible account of our data. It is equally possible that MLE integration occurred at a later stage of processing. In this account, a temporal order judgment is made within each sensory modality first. The left-hand auditory stimulus is compared to the right-hand auditory stimulus, and a parallel comparison occurs for the two tactile stimuli. These comparisons might occur in real time. All that is required is that the output of these comparisons carries quantitative information about the relative timing of left and right hand stimuli (i.e. left precedes right by 30 ms, rather than just left precedes right) and that information about precision is also produced. It would then be possible to perform MLE integration in a subsequent computation before reaching a decision.

Previous research assessing MLE models of audiovisual integration for a counting task (Andersen, Tiippana & Sams, 2004; 2005) has indicated that a model based on continuous representations of sensory inputs (like that assessed here) is superior to a

model based on discrete representations (often considered to be a kind of late integration). However, the late integration account outlined above still operates on continuous representations, because the magnitude of the left-right temporal asynchrony is represented following each unimodal comparison. Hence we cannot rule it out with a similar approach to that of Andersen et al. (2005). While the late integration account does not fit the phenomenology of the task (we were careful to produce stimuli that we felt combined plausibly into bimodal wholes) it remains viable. The interesting issue of whether TOJs are accomplished in real time (i.e. by comparing time of arrival at a decision centre) is therefore not resolved by the current data, but might inform future research comparing multisensory stimuli.

In summary, we have shown that performance on a bimodal temporal order judgment task with combined auditory-tactile stimuli is statistically indistinguishable from the predictions of an optimal MLE model of bimodal integration. Other simple models, suggesting that participants relied exclusively on audition or selected the best unimodal input on each trial, were rejected based on reliable differences between model predictions and observed behaviour. We therefore conclude that while the locus of integration remains uncertain, humans are nonetheless able to integrate auditory and vibrotactile information in a statistically optimal manner when determining the temporal order of bisensory events.

References

Alais, D. & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology, 14,* 257-262.

Andersen, T. S., Tiippana, K., & Sams, M. (2004). Factors influencing audiovisual fission and fusion illusions. *Brain Research: Cognitive Brain Research, 21,* 301-308.

Andersen, T. S., Tiippana, K., & Sams, M. (2005). Maximum Likelihood Integration of rapid flashes and beeps. *Neuroscience Letters, 380,* 155-160.

Bertelson, P. & de Gelder, B. E. M. (2004). The psychology of multimodal perception. In C. Spence & J. Driver (Eds.), *Crossmodal space and crossmodal attention* (pp. 141-178). Oxford: Oxford University Press.

Bertelson, P. & Radeau, M. (1981). Cross-modal bias and perceptual fusion with auditory-visual spatial discordance. *Perception and Psychophysics, 29,* 578-584.

Bresciani, J. P., Dammeier, F., & Ernst, M. O. (2006). Vision and touch are automatically integrated for the perception of sequences of events. *Journal of Vision, 6,* 554-564.

Bresciani, J. P. & Ernst, M. O. (2007). Signal reliability modulates auditory-tactile integration for event counting. *Neuroreport, 18,* 1157-1161.

Bresciani, J. P., Ernst, M. O., Drewing, K., Bouyer, G., Maury, V., & Kheddar, A. (2005). Feeling what you hear: auditory signals can modulate tactile tap perception. *Experimental Brain Research, 162,* 172-180.

de Lange, H. (1958). Research into the dynamic nature of the human fovea-cortex systems with intermittent and modulated light. I. Attenuation characteristics with white and colored light. *Journal of the Optical Society of America, 48,* 777-784.

Dennett, D. C. & Kinsbourne, M. (1992). Time and the observer: The where and when of consciousness in the brain. *Behavioral and Brain Sciences, 15,* 183-247.

Ernst, M. O. & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature, 415,* 429-433.

Ernst, M. O. & Bülthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences, 8,* 162-169.

Fujisaki, W., Shimojo, S., Kashino, M., & Nishida, S. (2004). Recalibration of audiovisual simultaneity. *Nature Neuroscience, 7,* 773-778.

Hanson, J. V., Heron, J., & Whitaker, D. (2008). Recalibration of perceived time across sensory modalities. *Experimental Brain Research, 185,* 347-352.

Hawken, M. J., Shapley, R. M. & Grosof, D. H. (1996). Temporal frequency selectivity in monkey visual cortex. *Visual Neuroscience, 13,* 477-492.

Heron, J., Whitaker, D., & McGraw, P. V. (2004). Sensory uncertainty governs the extent of audio-visual interaction. *Vision Research, 44,* 2875-2884.

Hillis, J. M., Watt, S. J., Landy, M. S., & Banks, M. S. (2004). Slant from texture and disparity cues: optimal cue combination. *Journal of Vision, 4,* 967-992.

Kitazawa S, Moizumi S, Okuzumi A, Saito F, Shibuya S, Takahashi T, Wada M, & Yamamoto S. (2007). Reversal of subjective temporal order due to sensory and motor integrations. In P. Haggard, M. Kawato & Y. Rossetti (Eds.) *Attention and Performance XXII* (pp. 73-97). Oxford: Oxford University Press.

Knill, D. C. & Pouget, A. (2004). The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends in Neurosciences, 27,* 712-719.

Miyazaki, M., Nozaki, D., & Nakajima, Y. (2005). Testing Bayesian models of human coincidence timing. *Journal of Neurophysiology, 94,* 395-399.

Miyazaki, M., Yamamoto, S., Uchida, S., & Kitazawa, S. (2006). Bayesian calibration of simultaneity in tactile temporal order judgment. *Nature Neuroscience, 9,* 875-877.

Morein-Zamir, S., Soto-Faraco, S., & Kingstone, A. (2003). Auditory capture of vision: examining temporal ventriloquism. *Brain Research: Cognitive Brain Research, 17,* 154-163.

Müller, J. (1838). *Handbook der Physiologie des Menschen [Handbook of Human Physiology]*. (vol. 2) Coblenz: J. Hölscher.

Navarra, J., Soto-Faraco, S., & Spence, C. (2007). Adaptation to audiotactile asynchrony. *Neuroscience Letters, 413,* 72-76.

Pick, H. L., Warren, D. H., & Hay, J. C. (1969). Sensory conflict in judgements of spatial direction. *Perception and Psychophysics, 6,* 203-205.

Recanzone, G. H. (2003). Auditory influences on visual temporal rate perception. *Journal of Neurophysiology, 89,* 1078-1093.

Roach, N. W., Heron, J., & McGraw, P. V. (2006). Resolving multisensory conflict: a strategy for balancing the costs and benefits of audio-visual integration. *Proceedings of the Royal Society of London B: Biological Sciences, 273,* 2159-2168.

Rock, I. & Victor, J. (1964). Vision and touch: An experimentally created conflict between the two senses. *Science, 143,* 594-596.

Rosenberger, W. F. & Grill, S. E. (1997). A sequential design for psychophysical experiments: an application to estimating timing of sensory events. *Statistics in Medicine, 16,* 2245-2260.

Scheier, C. R., Nijhawan, R., & Shimojo, S. (1999). Sound alters visual temporal resolution. *Investigative Ophthalmology and Visual Science, 40,* 169.

Shams, L., Kamitani, Y., & Shimojo, S. (2000). Illusions. What you see is what you hear. *Nature, 408,* 788.

Shams, L., Kamitani, Y., & Shimojo, S. (2002). Visual illusion induced by sound. *Brain Research: Cognitive Brain Research, 14,* 147-152.

Shams, L., Ma, W. J., & Beierholm, U. (2005). Sound-induced flash illusion as an optimal percept. *Neuroreport, 16,* 1923-1927.

Sherrick, C. E. (1976). The antagonisms of hearing and touch. In S. K. Hirsh, D. H. Eldredge, I. J. Hirsh, & S. R. Silverman (Eds.), *Hearing and Davis: Essays honoring Hallowell Davis* (pp. 149-158). Saint Louis, Missouri: Washington University Press.

Spence, C., Shore, D. I., & Klein, R. M. (2001). Multisensory prior entry. *Journal of Experimental Psychology: General, 130,* 799-832.

Sternberg, S. & Knoll, R. L. (1973). The perception of temporal order: Fundamental issues and a general model. In S. Kornblum (Ed.), *Attention and Performance IV* (pp. 629-686). London: Academic Press.

Ulrich, R. (1987). Threshold models of temporal-order judgments evaluated by a ternary response task. *Perception and Psychophysics, 42,* 224-239.

Van Beers, R. J., Sittig, A. C., & Gon, J. J. (1999). Integration of proprioceptive and visual position-information: An experimentally supported model. *Journal of Neurophysiology, 81,* 1355-1364.

Viemeister, N. F. (1979). Temporal modulation transfer functions based upon modulation thresholds. *Journal of the Acoustical Society of America, 66,* 1364-1380.

Wada, Y., Kitagawa, N., & Noguchi, K. (2003). Audio-visual integration in temporal perception. *International Journal of Psychophysiology, 50,* 117-124.

Weisenberger, J. M. (1986). Sensitivity to amplitude-modulated vibrotactile signals. *Journal of the Acoustical Society of America, 80,* 1707-1715.

Welch, R. B., DuttonHurt, L. D., & Warren, D. H. (1986). Contributions of audition and vision to temporal rate perception. *Perception and Psychophysics, 39,* 294-300.

Welch, R. B. & Warren, D. H. (1980). Immediate perceptual response to intersensory discrepancy. *Psychological Bulletin, 88,* 638-667.

Welch, R. B., Widawski, M. H., Harrington, J., & Warren, D. H. (1979). An examination of the relationship between visual capture and prism adaptation. *Perception and Psychophysics, 25,* 126-132.

Wichmann, F. A. & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception and Psychophysics, 63,* 1293-1313.

Wozny, D. R., Beierholm, U. R., & Shams, L. (2008). Human trimodal perception follows optimal statistical inference. *Journal of Vision, 8(3):24,* 1-11.

Appendix

Participant by participant predictions for the three models, alongside data obtained in bimodal conditions.

*Confidence intervals are based on a percentile parametric bootstrap method using 4999 simulations. * Only participants 1-24 were included in the main analysis. ** For experimental order 1a = unimodal auditory, 1t = unimodal tactile, 2 = bimodal.*

Predicted and observed tactile weights. This section shows predictions derived from the Rely on Audition and Best Sensory Estimate models.

Subject*	Age	Order*	Rely on Audition Model			Best sensory estimate model								
			All Tactile profiles			Gradual tactile profile			Intermediate tactile profile			Steep tactile profile		
			Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval	
				Low	High		Low	High		Low	High		Low	High
1	20	1a1t2	0	0	0	0	0	1	0	0	1	0	0	1
2	21	21a1t	0	0	0	0	0	1	0	0	1	0	0	1
3	27	1t1a2	0	0	0	0	0	0	0	0	1	1	0	1
4	24	21a1t	0	0	0	0	0	1	1	0	1	0	0	1
5	29	1a1t2	0	0	0	0	0	1	1	0	1	1	0	1
6	24	1t1a2	0	0	0	0	0	0	0	0	0	0	0	1
7	23	21t1a	0	0	0	0	0	0	0	0	0	0	0	0
8	25	1a1t2	0	0	0	0	0	1	1	0	1	1	1	1
9	29	1t1a2	0	0	0	0	0	1	0	0	1	1	0	1
10	22	21t1a	0	0	0	0	0	0	0	0	1	0	0	1
11	28	21t1a	0	0	0	0	0	0	0	0	1	0	0	1
12	23	1t1a2	0	0	0	0	0	1	1	0	1	1	0	1
13	22	21a1t	0	0	0	1	1	1	1	0	1	1	1	1
14	20	21t1a	0	0	0	0	0	1	0	0	1	0	0	1
15	25	1a1t2	0	0	0	0	0	1	1	0	1	1	0	1
16	33	21a1t	0	0	0	0	0	1	1	1	1	1	0	1
17	30	1t1a2	0	0	0	0	0	1	1	0	1	1	0	1
18	24	21t1a	0	0	0	1	0	1	1	0	1	1	1	1
19	32	21a1t	0	0	0	1	0	1	1	0	1	1	0	1
20	26	21t1a	0	0	0	1	1	1	1	0	1	1	1	1
21	20	1t1a2	0	0	0	0	0	1	1	0	1	1	1	1
22	28	21a1t	0	0	0	1	0	1	1	1	1	1	1	1
23	30	1a1t2	0	0	0	0	0	0	0	0	1	1	0	1
24	29	1a1t2	0	0	0	0	0	0	0	0	1	1	1	1
25	22	21a1t	0	0	0	1	0	1	1	1	1	1	0	1
26	29	1a1t2	0	0	0	0	0	0	0	0	1	1	0	1
27	23	1t1a2	0	0	0	0	0	1	1	1	1	1	1	1
28	19	1a1t2	0	0	0	0	0	0	0	0	0	0	0	0

Predicted and observed tactile weights. This section shows predictions derived from the MLE model, and the bimodal data.

Subject*	MLE model									Bimodal Data								
	Gradual tactile profile			Intermediate tactile profile			Steep tactile profile			Gradual tactile profile			Intermediate tactile profile			Steep tactile profile		
	Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval	
		Low	High		Low	High		Low	High		Low	High		Low	High		Low	High
1	0.47	0.12	0.85	0.25	0.05	0.66	0.28	0.07	0.67	0.46	-0.45	1.33	0.98	0.44	1.54	0.44	-0.38	1.07
2	0.10	0.00	0.53	0.25	0.02	0.69	0.20	0.02	0.62	0.64	-1.10	3.92	-0.28	-5.24	2.39	-0.04	-3.60	12.25
3	0.08	0.01	0.29	0.23	0.04	0.55	0.60	0.21	0.90	0.32	-0.60	0.98	-0.18	-1.21	0.62	0.22	-0.61	0.84
4	0.25	0.04	0.58	0.62	0.22	0.89	0.33	0.08	0.68	0.58	-0.13	1.28	0.40	-0.25	1.22	1.06	0.13	1.89
5	0.22	0.03	0.70	0.73	0.39	0.96	0.80	0.43	0.97	0.88	-0.01	2.40	0.88	-0.19	1.92	-0.64	-1.38	0.35
6	0.08	0.00	0.30	0.16	0.04	0.28	0.48	0.12	0.79	0.70	-0.01	1.38	0.84	0.26	1.36	1.00	0.49	1.41
7	0.01	0.00	0.07	0.02	0.00	0.12	0.11	0.01	0.38	-0.64	-1.59	0.35	0.58	-0.18	1.34	-0.60	-1.00	-0.21
8	0.49	0.18	0.86	0.62	0.26	0.92	0.90	0.71	0.99	-0.06	-0.71	0.75	0.36	0.16	0.89	0.70	0.14	1.27
9	0.03	0.00	0.56	0.41	0.02	0.90	0.81	0.44	0.98	-0.42	-2.45	1.11	0.88	-0.88	3.18	-0.14	-1.17	1.05
10	0.19	0.02	0.47	0.27	0.05	0.62	0.34	0.06	0.67	0.90	0.00	1.66	0.04	-0.78	0.93	0.82	0.15	1.39
11	0.07	0.00	0.25	0.44	0.04	0.90	0.27	0.02	0.69	-0.24	-0.66	0.25	0.26	-0.13	0.68	0.58	0.25	0.93
12	0.49	0.15	0.90	0.82	0.45	0.98	0.77	0.43	0.97	0.50	-0.27	1.26	0.80	-0.34	1.51	0.98	0.19	1.87
13	0.86	0.53	0.98	0.81	0.47	0.98	0.93	0.70	0.99	1.40	0.31	2.23	0.92	0.22	1.63	0.88	0.11	1.82
14	0.20	0.03	0.51	0.39	0.08	0.76	0.41	0.11	0.78	-0.20	-0.88	0.40	0.52	-0.05	0.89	-0.34	-0.98	0.36
15	0.30	0.00	0.96	0.52	0.11	0.98	0.77	0.30	0.99	-0.54	-2.48	1.24	1.62	0.22	3.19	0.54	-0.10	0.97
16	0.22	0.00	1.00	0.91	0.61	1.00	0.88	0.42	1.00	-1.22	-12.8	3.95	1.40	0.15	4.02	1.78	0.86	2.89
17	0.28	0.03	0.73	0.74	0.36	0.97	0.77	0.40	0.97	-0.38	-1.35	0.86	1.02	0.69	1.41	0.50	-0.01	1.10
18	0.50	0.18	0.89	0.73	0.38	0.96	0.85	0.57	0.98	2.30	0.32	5.10	0.98	0.11	1.63	1.54	0.71	2.40
19	0.62	0.14	0.92	0.83	0.49	0.98	0.73	0.27	0.95	2.56	1.11	3.78	0.90	-0.34	1.68	1.30	0.37	2.08
20	0.93	0.72	1.00	0.69	0.25	0.96	0.82	0.50	0.98	0.72	-0.20	1.44	0.84	0.09	1.56	0.56	-0.23	1.37
21	0.43	0.05	0.96	0.79	0.36	0.99	0.93	0.68	1.00	0.76	-0.80	2.54	0.06	-0.93	1.19	-0.12	-2.68	1.80
22	0.83	0.35	1.00	0.88	0.53	1.00	0.96	0.83	1.00	0.38	-0.37	1.10	0.58	0.07	1.23	0.56	0.03	1.36
23	0.08	0.01	0.30	0.29	0.04	0.64	0.56	0.20	0.86	0.86	-0.10	1.71	0.54	-0.47	1.50	0.70	-0.11	1.44
24	0.03	0.00	0.38	0.39	0.05	0.80	0.83	0.52	0.97	-0.98	-6.19	2.63	0.50	-0.92	1.84	0.82	-0.20	2.46
25	0.90	0.28	1.00	0.96	0.57	1.00	0.95	0.48	1.00	-0.76	-17.1	3.33	1.32	-0.58	2.48	0.36	-0.55	1.76
26	0.02	0.00	0.46	0.08	0.00	0.65	0.78	0.39	0.98	-0.80	-2.38	3.52	0.04	-1.67	1.82	-0.02	-1.14	1.23
27	0.31	0.00	0.97	0.92	0.63	1.00	0.92	0.58	1.00	-8.04	-2623	53.40	1.38	-301	121.11	1.62	-6.16	22.21
28	0.00	0.00	0.01	0.02	0.01	0.09	0.03	0.01	0.11	0.92	-0.16	1.62	0.38	-1.26	1.62	-0.08	-1.80	1.48

Predicted and observed judgment uncertainty. This section shows predictions derived from the Rely on Audition and Best Sensory Estimate models.

Subject*	Age	Order**	Rely on Audition Model			Best sensory estimate model								
			All tactile profiles			Gradual tactile profile			Intermediate tactile profile			Steep tactile profile		
			Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval	
				Low	High		Low	High		Low	High		Low	High
1	20	1a1t2	118	58	196	118	50	158	118	58	181	118	58	178
2	21	21a1t	154	78	296	154	78	287	154	78	266	154	78	272
3	27	1t1a2	79	35	108	79	35	108	79	35	105	65	24	82
4	24	21a1t	87	40	124	87	40	120	68	28	91	87	39	115
5	29	1a1t2	143	72	290	143	72	251	88	38	121	72	35	110
6	24	1t1a2	94	43	134	94	43	134	94	43	134	94	39	111
7	23	21t1a	37	14	57	37	14	57	37	14	57	37	14	56
8	25	1a1t2	113	56	194	113	49	136	88	37	117	37	9	51
9	29	1t1a2	254	125	695	254	125	647	254	117	418	122	62	198
10	22	21t1a	64	24	86	64	24	86	64	24	84	64	24	81
11	28	21t1a	33	7	45	33	7	45	33	4	40	33	6	44
12	23	1t1a2	163	82	389	163	72	218	77	36	123	89	42	129
13	22	21a1t	110	56	200	45	16	73	53	17	79	30	10	51
14	20	21t1a	72	32	108	72	31	105	72	30	97	72	29	91
15	25	1a1t2	147	68	868	147	68	317	140	65	215	81	43	132
16	33	21a1t	493	198	21056	493	198	2178	153	153	167	183	103	332
17	30	1t1a2	130	63	253	130	63	212	78	31	108	71	29	100
18	24	21t1a	168	89	346	167	77	216	102	49	155	71	33	107
19	32	21a1t	228	116	469	178	88	271	104	46	158	138	74	228
20	26	21t1a	202	99	523	54	22	85	136	66	211	94	41	135
21	20	1t1a2	269	130	1154	269	124	457	139	70	228	76	33	121
22	28	21a1t	330	152	1818	149	73	287	119	59	213	64	28	96
23	30	1a1t2	84	37	118	84	37	118	84	37	113	75	30	88
24	29	1a1t2	187	95	349	187	94	348	187	91	272	84	40	127
25	22	21a1t	882	240	495620	286	138	618	176	83	343	202	102	428
26	29	1a1t2	233	121	684	233	121	650	233	121	565	125	62	202
27	23	1t1a2	417	182	2268	417	166	1058	120	61	200	127	67	225
28	19	1a1t2	19	19	20	19	19	20	19	19	20	19	19	20

Predicted and observed judgement uncertainty. This section shows predictions derived from the MLE model, and the bimodal data.

Subject*	MLE model									Bimodal Data								
	Gradual tactile profile			Intermediate tactile profile			Steep tactile profile			Gradual tactile profile			Intermediate tactile profile			Steep tactile profile		
	Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval		Estimate	95% confidence interval	
		Low	High		Low	High		Low	High		Low	High		Low	High		Low	High
1	86	44	122	102	54	143	100	53	139	80	50	96	58	36	76	77	49	95
2	146	76	256	133	73	220	138	75	219	211	143	358	258	170	562	283	167	4620
3	76	35	99	69	33	87	50	22	63	70	46	90	81	51	99	51	33	68
4	75	38	99	54	26	69	71	36	90	86	60	116	65	42	80	82	51	102
5	126	68	203	75	36	99	64	33	91	120	92	164	97	61	114	74	49	94
6	90	42	124	86	42	114	68	35	86	62	38	71	48	29	56	39	21	46
7	37	14	56	37	14	55	35	14	50	98	67	132	66	39	77	43	29	56
8	81	43	105	69	34	92	35	9	46	56	35	74	31	14	37	35	19	46
9	250	123	590	194	103	353	110	59	163	205	129	648	177	115	275	108	73	158
10	58	23	74	55	23	66	52	23	64	76	47	93	58	38	76	53	33	65
11	32	7	41	25	4	31	28	6	35	36	21	43	28	15	35	28	16	35
12	116	64	171	70	34	102	78	40	107	72	45	84	75	49	96	75	48	91
13	42	15	61	48	17	66	29	10	45	92	62	122	79	51	103	70	45	90
14	64	30	87	56	28	75	55	27	69	60	37	71	59	40	73	53	33	68
15	123	63	273	101	56	179	71	40	112	169	110	710	93	59	199	66	44	94
16	435	187	1946	146	123	166	172	98	294	354	214	8397	154	102	241	114	74	171
17	110	59	172	67	29	88	62	29	82	118	85	180	44	37	52	42	24	49
18	118	67	168	87	46	126	65	32	94	135	90	231	60	37	74	81	50	94
19	140	79	219	95	44	131	118	68	180	152	102	223	89	59	117	76	46	94
20	52	22	78	113	60	173	85	40	116	81	54	109	54	33	68	62	42	77
21	204	111	377	123	66	192	73	32	111	140	93	213	114	77	153	141	95	272
22	136	70	240	112	57	183	63	28	91	63	38	74	44	26	55	49	30	65
23	81	37	109	71	35	92	56	27	67	82	54	109	89	54	109	67	42	79
24	184	93	326	146	82	220	77	39	107	215	145	1109	141	94	208	113	83	153
25	272	132	553	173	81	317	197	99	390	236	142	3146	175	122	283	114	77	149
26	231	119	592	223	119	517	110	59	168	154	97	253	159	107	232	103	67	135
27	346	149	944	115	61	180	121	65	201	668	340	603440	522	290	289290	323	196	13317
28	19	19	20	19	18	20	19	18	20	135	104	186	153	115	256	136	91	193

Tables

Table 1

Mean squared deviation of bimodal judgment uncertainties from the predictions of the MLE, best sensory estimate, and rely on audition models. Data are shown separately for the combination of the auditory stimulus with each of the three vibrotactile stimuli.

Model	Gradual tactile profile		Intermediate tactile profile		Steep tactile profile	
	MSD	SE	MSD	SE	MSD	SE
Rely on audition	6458	3045	13654	5600	15554	6492
Best sensory estimate	3078	1043	2001	566	1672	711
MLE	1539	393	1389	663	1534	875

Table 2

Mean squared deviation of bimodal tactile weights from the predictions of the MLE, best sensory estimate, and rely on audition models. Data are shown separately for the combination of the auditory stimulus with each of the three vibrotactile stimuli.

Model	Gradual tactile profile		Intermediate tactile profile		Steep tactile profile	
	MSD	SE	MSD	SE	MSD	SE
Rely on audition	0.95	0.33	0.62	0.13	0.67	0.16
Best sensory estimate	0.54	0.12	0.26	0.06	0.49	0.13
MLE	0.64	0.20	0.19	0.06	0.36	0.10

Figure Legends

Figure 1. Schematic of experimental stimuli and methods. A) Stimuli sent to auditory and vibrotactile actuators for the first eight participants. Gaussian windowed sine waves were embedded in low-frequency noise. The width of the Gaussian window and the peak intensity of the signal were manipulated to adjust discriminability. B) The approximate position of the actuators is shown alongside stimuli presented on an example trial from the bimodal phase of the experiment. Dashed lines indicate objects beneath the desktop. On this trial, the combined left hand stimulus is presented 100 ms after the right hand stimulus, which itself contains a small (25 ms) discrepancy between the unimodal auditory (bottom) and vibrotactile (top) components. This discrepancy was used to assess the weight given to vibrotaction in the overall judgment.

Figure 2. Judgment uncertainty in unimodal conditions. A) Illustration of sigmoid fitting, based on combined data from all 24 participants. The size of each data point provides a rough guide to the number of observations collected. Note that because an adaptive procedure was used to determine the range of asynchronies each subject received, the more extreme asynchronies were only delivered to more uncertain participants, and then only rarely, whereas the central asynchronies reflect judgments from all participants. This explains the apparent rise in uncertainty at the extremes of the graph. B) Mean judgment uncertainties across participants, determined by individual fits to each participant's data. Error bars denote standard errors.

Figure 3. Comparison of bimodal judgment uncertainty and model predictions for three models of bisensory integration. A) Illustration of sigmoid fitting, based on combined data from 24 participants in bimodal conditions without any between-modality asynchrony. The size of each data point provides a rough guide to the number of observations collected. See legend to Figure 2 for an explanation of noise at high absolute asynchronies. B) Mean bimodal judgment uncertainties across participants, determined by individual fits to each participant's data, and mean model predictions across participants, based on unimodal judgment uncertainties. Error bars denote standard errors.

Figure 4. Illustration of method for determining tactile weights, based on combined data from 24 participants in bimodal conditions with a steep vibrotactile component stimulus and a -25, 0 0r 25 ms asynchrony between the right hand auditory and vibrotactile component stimuli. The shift in the PSS is used to estimate the weight given to vibrotaction. The size of each data point provides a rough guide to the number of observations collected. See legend to Figure 2 for an explanation of noise at high absolute asynchronies.

Figure 5. Comparison of weights given to vibrotactile stimuli in bimodal conditions and model predictions for three models of bisensory integration. Mean vibrotactile weights across participants were determined by individual fits to each participant's data, while mean model predictions across participants are based on unimodal judgment uncertainties. Error bars denote standard errors.

Figure 1

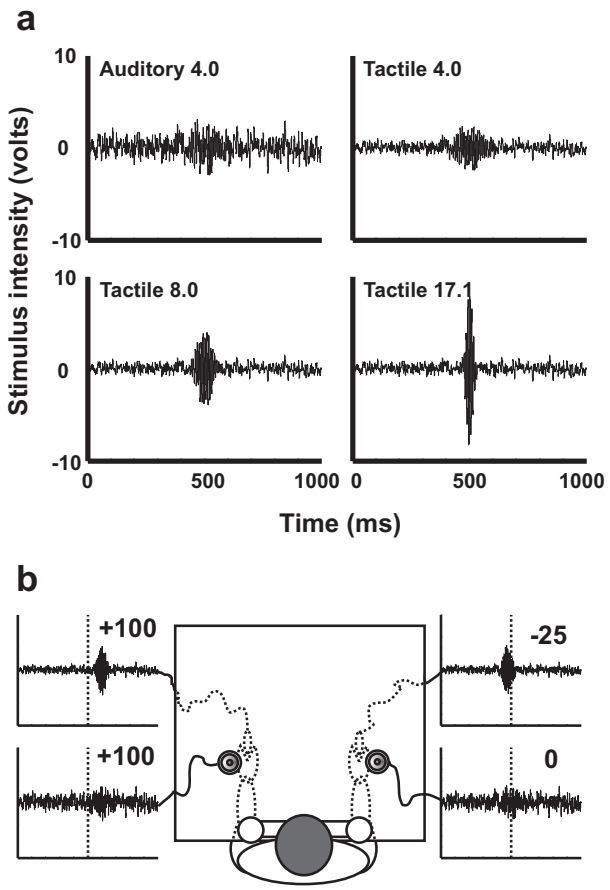

a
Auditory 4.0
Tactile 4.0
Tactile 8.0
Tactile 17.1
10
0
-10
Stimulus intensity (volts)
0
500
1000
Time (ms)
b
+100
+100
-25
0

Figure 2

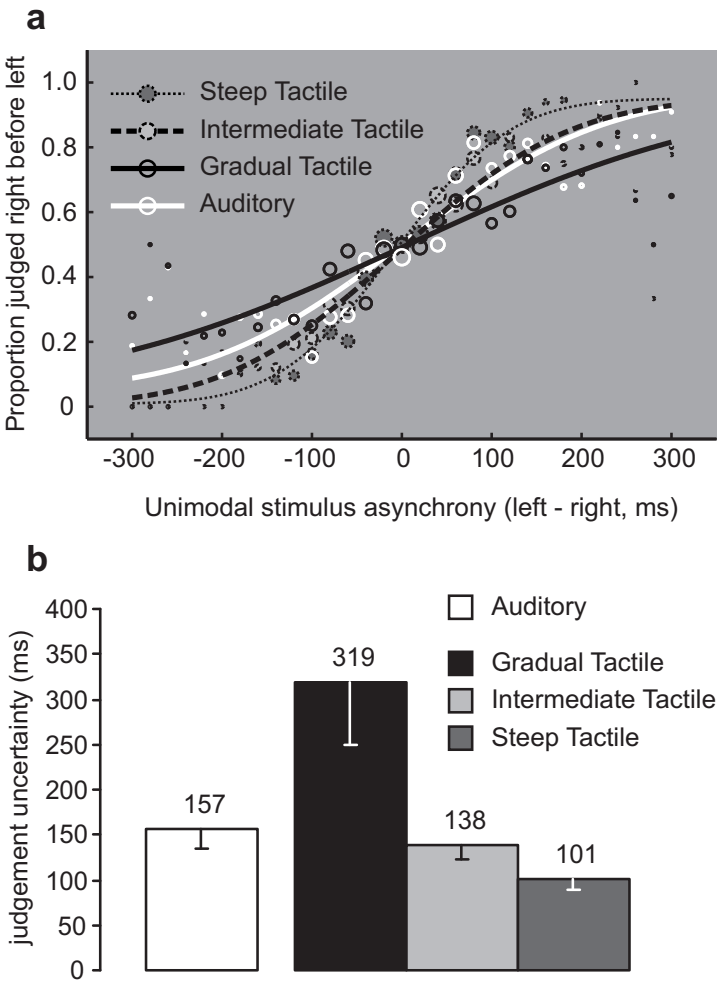

a
Steep Tactile
Intermediate Tactile
Gradual Tactile
Auditory
Proportion judged right before left
1.0
0.8
0.6
0.4
0.2
0
-300
-200
-100
0
100
200
300
Unimodal stimulus asynchrony (left - right, ms)
b
Auditory
Gradual Tactile
Intermediate Tactile
Steep Tactile
judgement uncertainty (ms)
400
350
300
250
200
150
100
50
0
157
319
138
101

Figure 3

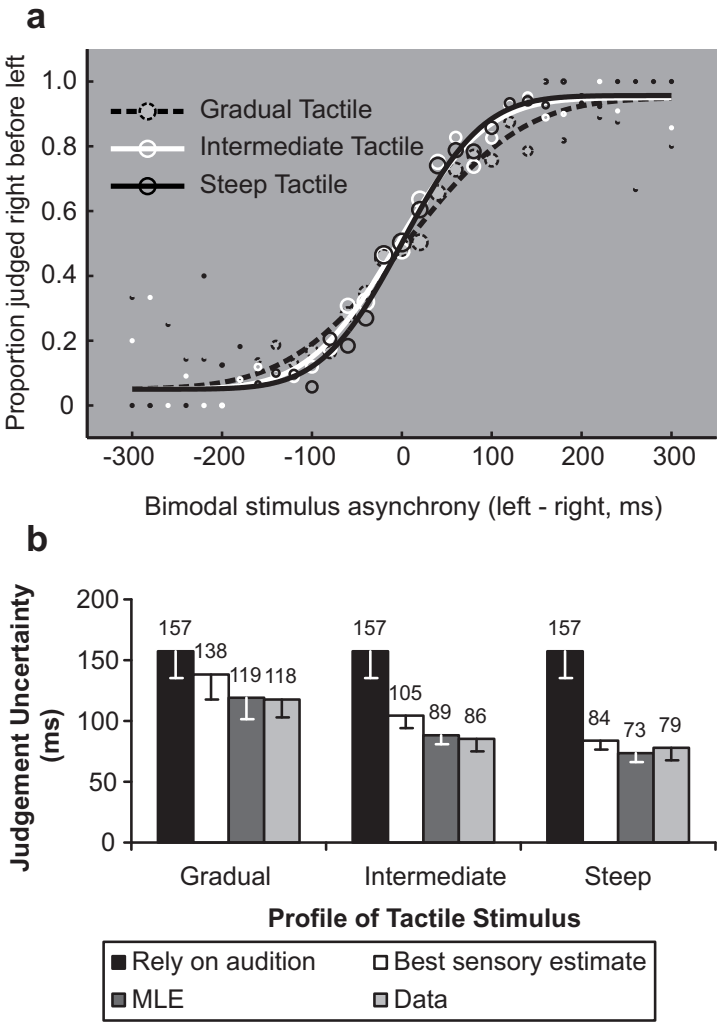

a
Proportion judged right before left
1.0
0.8
0.6
0.4
0.2
0
Gradual Tactile
Intermediate Tactile
Steep Tactile
-300
-200
-100
0
100
200
300
Bimodal stimulus asynchrony (left - right, ms)
b
Judgement Uncertainty (ms)
200
150
100
50
0
157
138
119
118
157
105
89
86
157
84
73
79
Gradual
Intermediate
Steep
Profile of Tactile Stimulus
Rely on audition
Best sensory estimate
MLE
Data

Figure 4

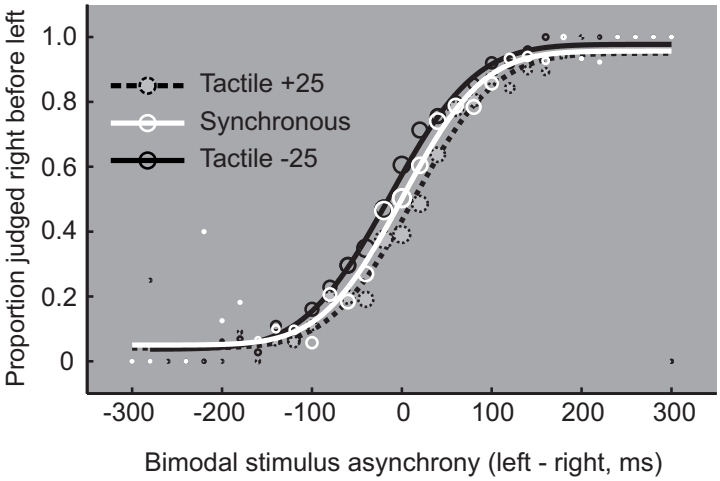
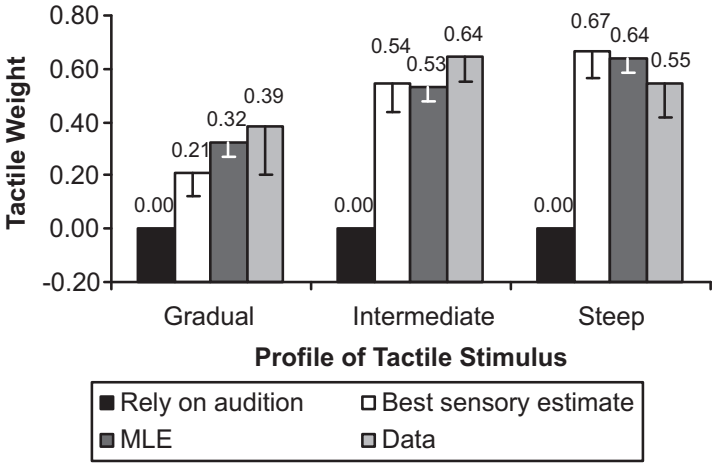

Proportion judged right before left
1.0
0.8
0.6
0.4
0.2
0
Tactile +25
Synchronous
Tactile -25
-300
-200
-100
0
100
200
300
Bimodal stimulus asynchrony (left - right, ms)

Figure 5


0.80
0.60
0.40
0.20
0.00
-0.20
Tactile Weight
0.00
0.21
0.32
0.39
0.00
0.54
0.53
0.64
0.00
0.67
0.64
0.55
Gradual
Intermediate
Steep
Profile of Tactile Stimulus
Rely on audition
Best sensory estimate
MLE
Data