Auditory–somatosensory multisensory interactions in front and rear space

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Abstract

The information conveyed by our senses can be combined to facilitate perception and behaviour. One focus of recent research has been on the factors governing such facilitatory multisensory interactions. The spatial register of neuronal receptive fields (RFs) appears to be a prerequisite for multisensory enhancement. In terms of auditory–somatosensory (AS) interactions, facilitatory effects on simple reaction times and on brain responses have been demonstrated in caudo-medial auditory cortices, both when auditory and somatosensory stimuli are presented to the same spatial location and also when they are separated by $100°$ in frontal space. One implication is that these brain regions contain large spatial RFs. The present study further investigated this possibility and, in particular, the question of whether AS interactions are restricted to frontal space, since recent research has revealed some fundamental differences between the sensory processing of stimuli in front and rear space. Twelve participants performed a simple reaction time task to auditory, somatosensory, or simultaneous auditory–somatosensory stimuli. The participants placed one of their arms in front of them and the other behind their backs. Loudspeakers were placed close to each hand. Thus, there were a total of eight stimulus conditions – four unisensory and four multisensory – including all possible combinations of posture and loudspeaker location. A significant facilitation of reaction times (RTs), exceeding that predicted by probability summation, was obtained following multisensory stimulation, irrespective of whether the stimuli were in spatial register or not. These results are interpreted in terms of the likely RF organization of previously identified auditory–somatosensory brain regions.
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1. Introduction

We simultaneously experience objects and events through multiple sensory channels that are specialized for transducing information concerning different aspects of our environments. These experiences are, in turn, combined to give rise to the integrated multisensory percepts that fill our daily lives. In the burgeoning literature on multisensory integration, many studies have highlighted the existence of extensive cross-modal links in information processing between the auditory and somatosensory modalities (e.g., Caclin, Soto-Faraco, Kingstone, & Spence, 2002; Guest, Catmur, Lloyd, & Spence, 2002; Jousmaki & Hari, 1998; Kitagawa, Zampini, & Spence, 2005; Soto-Faraco, Spence, & Kingstone, 2004; Spence, Nicholls, Gillespie, & Driver, 1998; Spence & Zampini, 2006; Turatto, Galfano, Bridgeman, & Umiltà, 2004; Zampini et al., 2005). Moreover, neurophysiological, neuropsychological, and electrophysiological studies have also demonstrated close links between the processing of auditory and somatosensory stimuli at the neural level (e.g., Caetano & Jousmaki, 2006; Eimer, Van Velzen, & Driver, 2002; Farnè & Làdavas, 2002; Foxe et al., 2000, 2002; Fu et al., 2003; Gobbelé et al., 2003; Hötting, Rösler, & Röder,

2003; Kujala et al., 1995; Lütkenhöner, Lammertmann, Simões, & Hari, 2002; Meredith, Nemitz, & Stein, 1987; Murray et al., 2005; Ortigue et al., 2005; Schroeder et al., 2001; Schurmann, Caetano, Hlushchuk, Jousmaki, & Hari, 2006; Stein & Meredith, 1993).

A considerable body of empirical research has investigated the principles governing multisensory integration and cross-modal interactions across species (see the chapters in Calvert, Spence, & Stein, 2004, for recent reviews). In animals, studies based primarily on electrophysiological recordings of neurons in the deep layers of the non-human mammalian superior colliculus have led to the formulation of several 'rules' of multisensory integration (Stein & Meredith, 1993; see also Stein, Stanford, Wallace, Vaughan, & Jiang, 2004). In particular, the so-called 'spatial rule' postulates that the multisensory enhancement of neural responses in many brain areas is dependent on the spatial alignment and/or overlap of a neuron's RFs. Importantly, facilitatory multisensory interactions (i.e., neuronal response enhancement) can be observed even when stimuli are spatially misaligned in their external positions, provided that the relevant neurons contain sufficiently large RFs, such that each stimulated position falls within their excitatory zones or provided that appropriate inputs have been established during development (Wallace & Stein, 2007). If this is not the case, no facilitation or even response depression can sometimes be observed.

Recent studies of auditory–somatosensory (AS) integration in the primate cortex have begun to address these issues and collectively suggest that the (temporally) earliest AS interactions most likely occur within the caudal-medial (CM) auditory belt cortices and can be elicited under anaesthesia, passive conditions, or tasks requiring simple detection responses. In humans, Foxe et al. (2000) observed non-linear neural response interactions in event-related potentials (ERP) recordings during a passive paradigm that included only spatially aligned stimulation of the left ear and left median nerve. These interactions began at ∼50 ms post-stimulus onset. In parallel, Schroeder et al. (2001) identified area CM in macaque monkeys as an auditory–somatosensory convergence zone (see also Fu et al., 2003). Both auditory and somatosensory stimuli, which were highly similar to those used by Foxe et al. (2000), were passively presented to awake animals and resulted in rapid, feed-forward response profiles in area CM (see Schroeder et al., 2003, for a review). Subsequent functional magnetic resonance imaging (fMRI) studies in humans under conditions of passive stimulation (Foxe et al., 2002) and in monkeys under anaesthesia (Kayser, Petkov, Augath, & Logothetis, 2005) have both shown supra-additive response interactions within area CM. Kayser et al. also provided evidence that such multisensory interactions depend upon temporal coincidence and obey an inverse effectiveness principle (reviewed by Stein & Meredith, 1993; though see Holmes & Spence, 2005).

Using ERPs and a simple RT task in humans, Murray et al. (2005) investigated whether spatially aligned and misaligned AS stimulus pairs, separated by 100°, share a common neural mechanism of multisensory integration. Their results showed that participants' RTs were facilitated for AS multisensory stimuli over either unisensory component stimuli and surpassed the

predictions based on probability summation (Miller, 1982), providing one kind of support for the neural integration of spatially misaligned AS pairs. Additionally, there was no evidence that the extent of facilitation varied as a function of the spatial alignment of the stimuli. That is, non-linear and supra-additive neural response interactions were observed ∼50 ms after the onset of the stimuli, irrespective of spatial alignment, and were explained by a modulation in the strength of responses of brain networks already active in the unisensory conditions. Distributed source estimations further localized these effects to area CM contralateral to the hand stimulated, irrespective of the position of sound in either the left or right frontal hemispace (Murray et al., 2005; see also Gonzalez Andino, Murray, Foxe, & de Peralta Menendez, 2005).

In view of the collective findings from different primate species, Murray et al. (2005) interpreted AS interactions, which occurred at similar latencies and within similar sources (both in the case of both spatially aligned and misaligned stimuli), in terms of the likely RF organization at a neural population level within area CM. Specifically, they postulated that area CM contains large bilateral auditory RFs and that somatosensory inputs from the hands are restricted to the contralateral hand.[1] Recent evidence from non-human primates supports this view and demonstrates that core, rostral, and caudal fields along the superior temporal plane are all responsive to the full 360° of azimuth, though it is also worth noting that the caudal fields demonstrated the highest degree of spatial tuning (Woods, Lopez, Long, Rahman, & Recanzone, 2006). A second conclusion supported by the collective evidence from studies of AS interactions in primates is that spatial influences (if present) likely manifest later in time in area CM and/or elsewhere in the brain than in area CM, because the effects summarized above were observed despite anaesthesia and irrespective of task requirements. More generally, Murray et al.'s (2005) study highlights how identifying the circumstances under which facilitatory interactions occur can provide insights into the likely organization of inputs onto structures (i.e., populations of neurons) contributing to multisensory integration.

The present study follows this line of research by investigating whether AS interactions during a simple speeded detection task are restricted to frontal space. Studies in both healthy and neuropsychological populations would suggest that AS interactions may be more prevalent in rear space (Farnè & Làdavas, 2002; Kitagawa et al., 2005; Zampini et al., 2005; see also Fu et al., 2003; Graziano, Reiss, & Gross, 1999, for data from macaques; see Kitagawa & Spence, 2006, for recent review). In these studies, effects such as cross-modal extinction and cross-modal interference on spatial discrimination tasks were larger when the stimuli were presented from rear space. That is, in all of these studies, the effects of AS interactions in rear space

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[1] We would note that evidence from non-human primates also indicates that area CM receives somatosensory inputs from representations of the face, neck, and arm (Fu et al., 2003), as well as the foot (Kayser et al., 2005). It will therefore be of particular interest for future research to conduct similar investigations in humans to determine the particular body surface(s) represented within area CM and elsewhere.

were shown to have a deleterious effect on behavioural performance. However, to date, no study has examined facilitatory effects of AS interactions in rear space. We therefore examined the redundant signals effect (RSE; i.e., faster responses for multisensory stimuli than for either unisensory stimulus presentation) from AS pairs of stimuli compared to unisensory auditory and somatosensory stimuli when they were presented in front and rear space. We also assessed whether the relative spatial position of the multisensory stimulus pairs modulates behavioural indices of multisensory interactions. To this end, AS stimulus pairs were presented to either the same or different positions in front of and/or behind the participants who performed the task with one arm in front of them and the other behind them.

2. Methods

2.1. Participants

Twelve right-handed participants (Oldfield, 1971; four males and eight females; mean age of 22 years; range from 19 to 29 years) were recruited to take part in the experiment, which took approximately 50 min to complete. All of the participants reported normal hearing and normal somatosensory sensitivity. None of the participants had a history of neurological or psychiatric disorder. The participants were naïve as to the purposes of the study. The experiments reported here were conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki, as well as the ethical guidelines laid down by the Department of Cognitive Sciences and Education, University of Trento. The participants gave their informed consent to participate in the study prior to the start of their experimental session.

2.2. Apparatus and stimuli

Somatosensory stimuli were delivered via Oticon-A 100 Ω bone conduction vibrators (1.6 cm × 2.4 cm; Oticon Inc., Somerset, NJ) driven by a white noise generator (82 dB(A)). Participants held the vibrators between the thumb and index finger of each hand. To further ensure that somatosensory stimuli were inaudible, continuous white noise was presented (75 dB(A) as measured from the participants' head position) from two loudspeaker cones (VE100AO, Audax, France), one placed 10 cm in front of the frontal tactile stimulator and the other placed 10 cm behind the rear tactile stimulator. The auditory stimuli consisted of 50 ms white noise bursts (82 dB(A) as measured from the participants' head position) delivered through loudspeaker cones (VE100AO, Audax, France) located next to the participants' hands (i.e., 1 cm from the tactile stimulators). These loudspeakers were not the same ones as used to deliver the continuous white noise. Participants' hands were positioned one in front and the other behind their back both at a distance of 70 cm from both of the participants' ears (see Fig. 1 for a schematic view of the experimental paradigm). Each of the eight stimulus configurations was randomly presented with equal frequency in blocks of 80 trials. Each participant completed eight blocks of trials, allowing for 80 trials of each stimulus type. The inter-stimulus interval varied randomly in the range 1.5–2.5 s.

2.3. Design

The participants were presented with the following stimulus conditions: (a) somatosensory stimuli alone, (b) auditory stimuli alone, (c) spatially 'aligned' auditory–somatosensory stimulation where both stimuli were simultaneously presented from the same location (e.g., somatosensory stimulation of the hand located in front of the participant and auditory stimulation of the loudspeaker located in front of the participant), and (d) spatially 'misaligned' auditory–somatosensory stimulation presented to different locations (e.g., front hand and rear loudspeaker). The nomenclature for the misaligned conditions is in terms of the location of the auditory stimulus. For example, 'misaligned front' refers to the combined presentation of an auditory stimulus from in front of the participant and a somatosensory stimulus from behind. There were eight configurations of stimuli in total, such that there was an equal probability of unisensory and multisensory conditions and that both front and rear presentations were counterbalanced (see Fig. 1). Which hand participants placed in front was counterbalanced across blocks of trials to ensure that effects followed from the spatial positions of the hands (i.e., in front or rear) rather than any differences between somatosensory sensitivity of the hands. The hand that was initially placed in front was counterbalanced across participants.
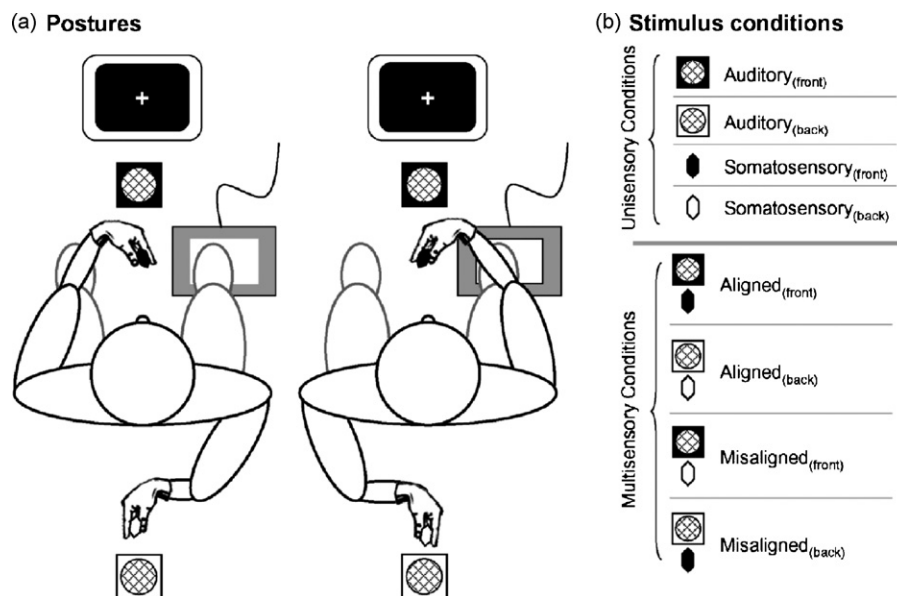

Fig. 1. Experimental paradigm. (a) Participants sat comfortably in a darkened room, centrally fixating a computer monitor and responding via a footpedal. The vibrotactile stimulators were held between the thumb and index finger of either hand. Loudspeaker cones were placed next to each hand. Stimuli presented from the front are coded by black symbols while those in rear space are represented by white symbols. (b) Stimulus conditions. There were a total of eight stimulus conditions: four unisensory and four multisensory. The multisensory conditions were counterbalanced for the spatially aligned and misaligned stimulus combinations.

2.4. Procedure

Participants sat in darkness in a quiet experimental booth and were instructed to keep their eyes closed and to make simple RT responses to detect any stimulus by means of a pedal located under their right foot. They were asked to emphasize speed, but to refrain from making anticipatory responses. Only RTs between 150 and 1000 ms were considered valid (cf. Murray et al., 2005). The participants completed two practice blocks (16 trials each; one block for each posture) to familiarize them with the paradigm. Stimulus delivery and response recordings were controlled by E-prime (Psychology Software Tools Inc.; www.pstnet.com/eprime).

3. Results

On average, participants detected 98.5 ± 1.8 percent ($\pm SD$ indicated) of all auditory stimuli, 99.2 ± 1.1 percent of the somatosensory stimuli, and 97.5 ± 2.2 percent of the AS multisensory stimulus pairs. On average, 98.2 ± 1.6 percent of the trials from any given participant were included in the analyses (range: 94.7–100 percent). RT performance for the unisensory stimuli and for both the spatially aligned and the spatially misaligned stimulus pairs were analyzed via two separate multivariate analyses of variance (ANOVAs). The first analysis tested for a RSE for spatially aligned stimulus pairs over unisensory stimuli. The within-participant factors were stimulus type (auditory-alone, somatosensory-alone, AS multisensory pair) and spatial location (front, rear). This analysis revealed significant main effects of stimulus type ($F_{(2,10)} = 148.36$; $p < .0001$) and spatial location ($F_{(1,11)} = 22.00$; $p < .001$), and a significant interaction between these two factors ($F_{(2,10)} = 11.64$; $p < .002$). Follow-up comparisons revealed the basis for these results (see Table 1). Participants responded significantly more rapidly to multisensory stimuli than to either unisensory counterpart no matter whether the stimuli were presented from the front or rear. This result is indicative of a RSE for both front and rear spatial locations. In addition, RTs were significantly faster for sounds presented from in front of the participants than from behind them. By contrast, there was no significant difference in RTs to tactile stimuli as a function of the spatial location from which they were presented.

The second ANOVA tested for a RSE with the spatially misaligned stimulus pairs. The within-participant factors were stimulus type (auditory-alone, somatosensory-alone, AS multi-

sensory pair) and spatial location (here the data were coded in the ANOVA such that the level 'front' included the auditory-alone in front, somatosensory-alone from the rear, and the misaligned-front conditions). The analysis revealed significant main effects of stimulus type ($F_{(2,10)} = 101.55$; $p < .0001$) and spatial location ($F_{(1,11)} = 31.11$; $p < .0001$), as well as a significant interaction between these two factors ($F_{(2,10)} = 6.33$; $p < .02$). As above, follow-up comparisons revealed the basis for these results (see Table 1). RTs were significantly faster for AS stimulus pairs than for either unisensory counterpart stimulus. This constitutes a demonstration of a RSE with misaligned AS multisensory stimulus pairs across front and back spatial locations. These follow-up contrasts also revealed that unisensory and multisensory conditions including auditory stimuli presented to the front of the participant were significantly faster than those when the sound was presented from behind, with no significant difference between front and rear tactile conditions.

A third ANOVA was conducted to determine if the mean RTs were faster for spatially 'aligned' versus 'misaligned' AS stimulus pairs. The within-participant factors were stimulus type (aligned vs. misaligned) and spatial location of the auditory stimulus (front vs. back). Neither the main effect of stimulus type ($F_{(1,11)} = 0.66$; *ns*) nor the interaction between these two factors ($F_{(1,11)} = 0.86$; *ns*) reached significance. However, there was a significant main effect of the spatial location of the auditory stimulus ($F_{(1,11)} = 11.81$; $p = .006$). This resulted from the fact that faster RTs were observed for those conditions in which the sound was presented from the front (i.e., 'aligned front' and 'misaligned front') than when it was presented from the rear (i.e., 'aligned back' and 'misaligned back').

Two broad classes of models can be used to explain instances of the RSE: race models and co-activation models. According to race models (Raab, 1962), neural interactions are not required to obtain the RSE. Rather, stimuli independently compete for response initiation and the faster of the two mediates behaviour on any given trial. Thus, simple probability summation could produce the RSE, since the likelihood of either of the two stimuli yielding a fast RT on any given trial is higher than that from either stimulus alone. According to co-activation models (e.g., Miller, 1982), neural responses from stimulus pairs interact and are pooled prior to behavioural response initiation, the threshold

Table 1

Results of follow-up planned comparisons between mean RTs for AS stimulus pairs and each of the constituent unisensory stimuli

| Stimulus configuration	RSE?	Auditory–somatosensory multisensory stimulus pair (ms)	Constituent unisensory stimulus	t-Value$_{(df)}$; p-value
Aligned front	√	238	Auditory$_{(front)}$: 268 ms Somatosensory$_{(front)}$: 283 ms	$t_{11} = 7.55$; $p < 1 \times 10^{-5}$ $t_{11} = 8.41$; $p < 4 \times 10^{-6}$
Aligned back	√	246	Auditory$_{(back)}$: 290 ms Somatosensory$_{(back)}$: 280 ms	$t_{11} = 8.71$; $p < 3 \times 10^{-6}$ $t_{11} = 12.17$; $p < 1 \times 10^{-7}$
Misaligned front	√	237	Auditory$_{(front)}$: 268 ms Somatosensory$_{(back)}$: 280 ms	$t_{11} = 9.11$; $p < 2 \times 10^{-6}$ $t_{11} = 10.88$; $p < 4 \times 10^{-7}$
Misaligned back	√	250	Auditory$_{(back)}$: 290 ms Somatosensory$_{(front)}$: 283 ms	$t_{11} = 7.82$; $p < 8 \times 10^{-6}$ $t_{11} = 9.68$; $p < 1 \times 10^{-6}$

Note that all comparisons were significant.

for which is met more rapidly by stimulus pairs than by single stimuli.

We tested whether the RSE exceeded the facilitation predicted by probability summation using Miller's inequality (Miller, 1982). Detailed descriptions of this analysis have been described in several previous reports (e.g., Murray, Foxe, Higgins, Javitt, & Schroeder, 2001; Murray et al., 2005). Briefly, the analysis entails calculating the probability distribution for each condition and participant. These distributions are first normalized in terms of the percentile of the range of RTs for each participant across all conditions (in the present study, bin widths of 5 percent were used). A model of the probability distribution for each spatial configuration of multisensory stimuli was then calculated. For each 5 percent bin, the modelled value equals the sum of the probabilities for each constituent unisensory condition minus their joint probability [i.e., $p(A) + p(S) - p(A) \times p(S)$]. This model represents the upper limit that would be explainable by probability summation and can be contrasted with the probability distribution actually obtained in response to multisensory stimulation. When the actual probability is greater than the modelled value, the race model is violated and probability summation cannot account for the RSE obtained. In all cases, we observed a violation of the race model (i.e., values greater than zero) over the fastest 15–20 percent of the RT distribution, thus supporting co-activation accounts of the present RSE (see Fig. 2b).[2]

Race model violation was statistically evaluated with a paired t-test (one-tailed) between the actual and modelled probability distributions. For the 'aligned front' condition, the actual values were significantly greater than the modelled values at the 10 percent ($t_{(11)} = 2.24$; $p = .023$) and 15 percent ($t_{(11)} = 1.95$; $p = .039$) percentiles of the probability distribution. For the 'aligned back' condition, the actual values were significantly greater than the modelled values at the 5 percent ($t_{(11)} = 2.76$; $p = .009$), 10 percent ($t_{(11)} = 3.39$; $p = .003$), 15 percent ($t_{(11)} = 2.00$; $p = .035$), and 20 percent ($t_{(11)} = 3.11$; $p = .005$) percentiles of the probability distribution. For the 'misaligned front' condition, the actual values were significantly greater than the modelled values at the 5 percent ($t_{(11)} = 3.12$; $p = .005$), 10 percent ($t_{(11)} = 3.01$; $p = .006$), and 15 percent ($t_{(11)} = 2.66$; $p = .011$) percentiles of the probability distribution. For the 'misaligned back' condition, the

(a) **Mean Reaction Times**
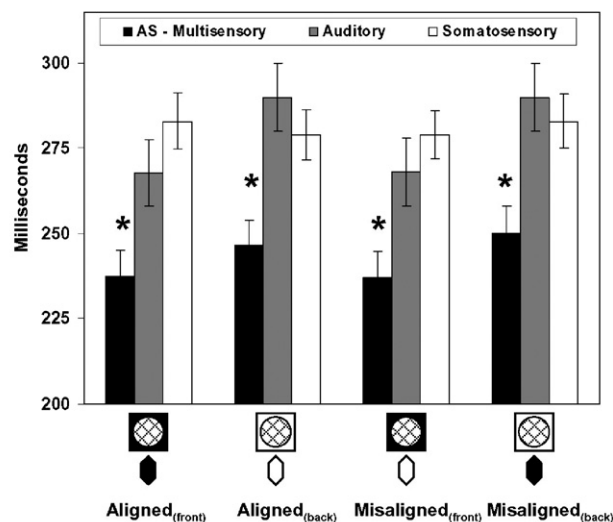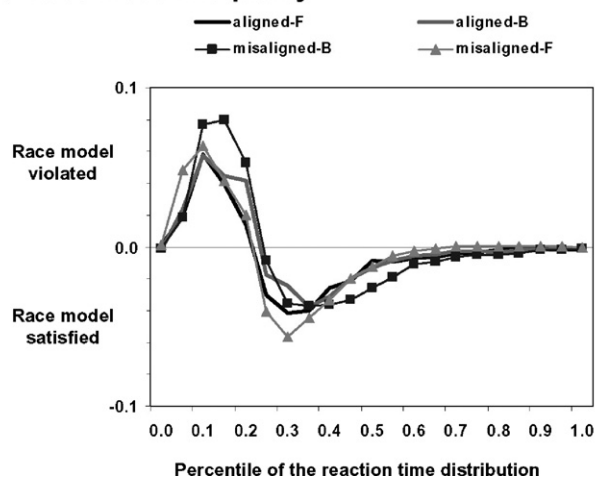
(b) **Race Model Inequality**

Fig. 2. Results. (a) Mean reaction times (standard error shown) for auditory–somatosensory multisensory pairs (black bars) and the corresponding auditory and somatosensory unisensory stimuli (gray and white bars, respectively). Asterisks indicate that an RSE was observed for a given spatial combination. (b) Results of applying Miller's (1982) inequality to the cumulative probability of RTs to each of the multisensory stimulus conditions and its unisensory counterparts. This inequality tests the observed RT distribution against that predicted by probability summation of the race model. Positive values indicate violation of the race model, and negative its satisfaction.

actual values were significantly greater than the modelled values at the 5 percent ($t_{(11)} = 3.53$; $p = .002$), 10 percent ($t_{(11)} = 4.19$; $p = .001$), 15 percent ($t_{(11)} = 3.90$; $p = .001$), and 20 percent ($t_{(11)} = 3.11$; $p = .005$) percentiles of the probability distribution.

4. Discussion

The results of the present study show that participants' behavioural responses were facilitated when they were presented with AS multisensory stimulus pairs relative to when they were presented with either of the constituent unisensory stimuli. This facilitation of RTs is indicative of a RSE for multisensory stimuli (e.g., Forster, Cavina-Pratesi, Aglioti, &

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[2] It is important to note that this model does not assess the equivalence of multisensory interactions with their unisensory counterparts (i.e., the relative benefit of multisensory stimulus pairs versus redundant unisensory stimulus pairs). Rather, it specifically queries whether the RT facilitation following multisensory stimulus presentation exceeds that which could be explained solely by the independent processing of each unisensory stimulus if presented alone. Violation of this inequality is a metric of interactive processing of multisensory stimuli and provides no comparison of multisensory integration and unisensory integration. It would be neither appropriate nor informative to compare probability distributions from multisensory conditions with those from double unisensory (e.g., auditory–auditory or somatosensory–somatosensory) conditions. For one, this is because the stimulus energies of these conditions differ. Second, the underlying neurophysiology for multisensory and unisensory interactions differs. Thus, even if one were to assess the equivalent of RSEs for multisensory and unisensory stimulus pairs, it would not be informative in terms of the underlying mechanism.

Berlucchi, 2002; Gondan, Niederhaus, Rösler, & Röder, 2005; Miller, 1982; Molholm et al., 2002; Murray et al., 2005; Schröger & Widmann, 1998). It is important to note that the present RSE occurred regardless of the spatial location from which the stimuli were presented or the specific body posture adopted by participants. Mean RTs were faster for AS multisensory stimulus pairs than for either unisensory auditory or unisensory somatosensory stimuli for both spatially aligned and spatially misaligned configurations. Additionally, there was no evidence of differences in participants' RTs to AS multisensory stimuli as a function of the spatial alignment of the stimuli. These results are consistent with (and extend) the findings reported by Murray et al. (2005), wherein no spatial modulation was observed when the auditory and somatosensory stimuli were presented from directly in front of the participants on either the same or opposite sides of the frontal midline (at a spatial separation of 100°). The present results thus demonstrate facilitatory AS interactions in rear space and raise the possibility that previously identified brain regions mediating AS multisensory interactions contain a RF organization that includes rear space.

In the present study, the facilitation of behavioural responses to multisensory over unisensory stimulation for both spatially aligned and misaligned combinations of AS stimulus pairs was found to be greater than would be expected on the basis of probability summation as described by a race model explanation. RSEs that violate the race model can be attributed to the facilitatory convergence of neural responses to the stimuli at some processing stage prior to the generation of a motor response. This convergence contrasts with race model accounts that posit that motor responses are initiated by the faster of two signals that independently engage sensory-motor processing pathways. The evidence for the race model violation found in the present study suggests neural co-activation both when stimuli are spatially aligned and spatially misaligned, no matter whether the stimuli are presented to either front or rear space.[3] The present results are thus distinct from those reported in studies using auditory and visual stimulus combinations. In these studies of both human (e.g., Frens, Van Opstal, & Van der Willigen, 1995; Gondan et al., 2005; Harrington & Peck, 1998) and animal behaviour (Stein, Meredith, Huneycutt, & McDade, 1989; also Stein & Meredith, 1993 for review), performance enhancement on simple detection tasks is reduced or absent when a spatial separation is introduced between the stimuli. More specifically, RT facilitation in excess of probability summation was consistently observed only when the auditory and visual stimuli were separated by less than 30°, with no subject showing race-model violation when stimuli were separated by 40° (cf. Fig. 3 of Harrington & Peck, 1998). One speculative possibility is that AS interactions may be inherently non-spatial (see also Kitagawa et al., 2005).

Consistent behavioural findings were reported by Murray et al. (2005). In their study, RTs were similarly facilitated for mul-

[3] However, it is important to note that non-linear neural response interactions have also been observed even when RT facilitations was fully accounted for by the race model account (Murray et al., 2001), as well as when passive tasks have been used (Foxe et al., 2000, 2002).
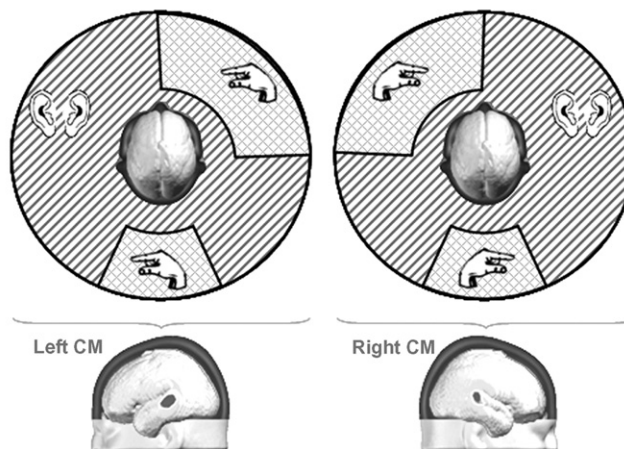
Putative Receptive Field Organization

Fig. 3. Putative RF organization at a population level within area CM. Our results, in conjunction with prior research (Murray et al., 2005), support a model wherein caudal-medial brain regions of the human superior temporal cortex contain large auditory RFs encompassing 360° of peripersonal space and somatosensory RFs for the contralateral hand, which can be positioned in front and rear space as shown. Somatosensory RFs are shown only for hand positions that have to date been tested. It is further likely to be the case that area CM also contains somatosensory inputs from other body surfaces, though such have not been thoroughly examined yet in humans (cf. Menning, Ackermann, Hertrich, & Mathiak, 2005).

tisensory pairs to a degree that exceeded race model predictions for all spatial combinations tested within frontal peripersonal space. They also reported electrophysiological correlates of these AS interactions. In their study, non-linear AS interactions were observed for both aligned and misaligned stimulus pairs over the 54–94 ms post-stimulus interval. These interactions were localized to area CM contralateral to the hand stimulated, regardless of the position of the sound in either the left or right hemispace (Gonzalez Andino et al., 2005; Murray et al., 2005; see also Fu et al., 2003 and Kayser et al., 2005, for similar evidence from macaque monkeys). Murray et al. interpreted these results as suggesting that the representations within area CM include unilateral somatosensory RFs and bilateral auditory RFs, such that somatosensory input originates from the contralateral hand and auditory inputs originate from both ipsi- and contralateral space. To the extent that the present results also involve non-linear neural response interactions within CM, our findings would further suggest that area CM contains auditory RFs that include both frontal and rear peripersonal space (i.e., 360°; note that this notion has been supported by recent electrophysiological findings in monkeys; Woods et al., 2006), and somatosensory RFs that encompass the contralateral hand irrespective of the body posture adopted (see Fig. 3).

An important aspect of the present study is that no explicit spatial processing or localization of the stimuli was required by our participants. As such, one can envisage that AS interactions in the present study dramatically differ from what would be expected under conditions where spatial information is task-relevant (Spence et al., 1998; Spence, McDonald, & Driver, 2004). For example, it might be the case that task requirements and/or attentional mechanisms exert a top-down influence

on neural response properties, such that neurons or populations of neurons emphasize the temporal profile of responses over their spatial tuning. Such dynamism of response properties has indeed been demonstrated within audition (Andersen & Buneo, 2002; Jay & Sparks, 1987) and vision (e.g., Tolias et al., 2001; Worgotter & Eysel, 2000), though to our knowledge similar findings following multisensory stimulation have yet to be demonstrated. On a related note, the position of effecter organs (e.g., arms, head, eyes, etc.) has been shown to influence RF properties (and most likely multisensory interactions; e.g., Werner-Reiss, Kelly, Trause, Underhill, & Groh, 2003); although recent studies would suggest that such effects within primary and belt auditory cortices are mediated by feedback influences (Fu et al., 2004). That said, we would like to iterate the fact that, in the present study, participants had to maintain central fixation as well as their posture during each block of trials. Despite these considerations, it is nonetheless our contention that any such top-down or task-related influences are modulating the responsiveness of anatomically defined AS interactions, at least within area CM where the initial effects are thought to occur.

One might similarly question the utility of a simple RT task in terms of evaluating the putative population-level RF organization of multisensory brain regions. That studies in non-human primates have documented AS integration within area CM despite the measurements being made under anaesthesia and/or passive conditions is suggestive of a certain degree of automaticity in AS integration at least within area CM (Fu et al., 2003; Kayser et al., 2005). This notion is further supported by the observation that both the auditory and somatosensory inputs into area CM exhibit timing as well as laminar distributions that are consistent with feedforward activations (Schroeder et al., 2001). That is, the capacity for neural integration appears to be both automatic and intrinsic to the underlying neurophysiology of the auditory and somatosensory systems, such that task-related and attention-related effects may modulate the activity within this architecture only via feedback mechanisms and/or at later stages of sensory-cognitive processing. A natural extension of this evidence for automatic AS integration relates to the question of how the spatial position/alignment of stimuli alters AS integration, though other factors, such as temporal synchrony and the general effectiveness of stimuli are also proving similarly informative (cf. Kayser et al., 2005).

Conceptually, this is akin to investigations of RF mapping wherein anatomically defined representations of the inputs to the sensory epithelia are identified in brain structures (reviewed in Stein & Meredith, 1993, for the case of multisensory integration). However, posing such questions in human participants under passive conditions and in the absence of physiological measurements would be problematic, since attention and arousal would constitute uncontrolled factors. In part for this reason, and also to obtain a metric of integrative processing (i.e., violation of Miller's race model inequality), we had our participants perform a simple detection task (see also Harrington & Peck, 1998). One presupposition inherent in this approach is that the present behavioural effects manifest as interactions within area CM. This remains to be empirically validated, and indeed this is the topic of ongoing electrophysiological research by our research groups. Still, a strong hypothesis from the extant literature is that the present paradigm results from AS interactions within CM. A further extension of the present study will be the introduction of spatial contingencies to the task, which will be used to assess whether (and if so, how) the required brain networks change/expand or are otherwise modified. As such, a simple RT task is not only an essential first step in the investigation of multisensory integration, but also an appropriate method for investigating spatial constraints, particularly when such processing is thought to proceed automatically (which the abovementioned studies in both animals and humans would indicate to be the case for AS interactions). That is, a limitation of a spatial task would be that it reveals AS interactions specifically in the context of additional top-down, attention-related, and task-related constraints; whereas a simple RT task would not include such constraints and identifies the widest possible extent of AS interactions (cf. Spence et al., 1998, on this issue). An additional and by no means mutually exclusive possibility is that behaviourally relevant AS interactions might also be occurring elsewhere in the brain, such as parietal cortices where spatial functions are though to be mediated (e.g., Andersen & Buneo, 2002, for review). However, the requisite experiments have not, as yet, been conducted. The only fMRI study of AS interactions in humans was conducted under passive conditions (Foxe et al., 2002), and EEG studies that included a simple detection task and that applied distributed source estimations have not found evidence for parietal involvement in AS interactions (Murray et al., 2005), even when these analyses were conducted on single-trial and single-participant data (Gonzalez Andino et al., 2005). Future experiments that require spatial analysis of the stimuli will clearly be informative in resolving the behavioural significance of any AS interactions within area CM.

To the best of our knowledge, this is the first demonstration of facilitatory effects of multisensory interactions in rear space. These results therefore provide novel information concerning the spatial limitations on facilitatory AS interactions. Other studies have investigated the effects of presenting auditory and somatosensory stimuli in the space behind the head. For example, Farnè and Làdavas (2002) reported AS extinction effects for stimuli presented in rear space. In this study, the patients failed to report the majority of the somatosensory stimuli presented on the contralesional side when an auditory stimulus was presented simultaneously on the ipsilesional side, even though they could report contralesional somatosensory stimuli near-perfectly when presented in isolation. Kitagawa et al. (2005) reported a spatial modulation of AS temporal order judgments (TOJs) when stimuli were presented in the region behind the head. Participants' performance was better when the auditory and somatosensory stimuli were presented from different spatial positions than when they were presented from the same spatial position. In a separate experiment, they also demonstrated that speeded spatial discrimination (left vs. right) responses to somatosensory stimuli presented in rear space are modulated by the spatial congruency of auditory distractors (i.e., presented on the same versus opposite side). However, neither of these studies revealed (nor did they look for) any AS response

enhancement when multisensory stimuli were presented in rear space.

These lines of evidence have been taken to suggest that AS interactions may be more prevalent in rear space (i.e., in the region where vision provides no direct information) than in frontal space. Farnè and Làdavas (2002) have argued that this is because people will typically perceive an object's approach from behind by means of auditory cues (see also Kitagawa & Spence, 2006). The investigation of possible spatial modulation effects during the performance of a simple RT task when AS stimuli are restricted to rear space will therefore be important for future research aimed at describing spatial influences on attention and discrimination performance. It is further interesting to note that all previous studies that have shown a spatial modulation of AS interactions have presented somatosensory stimuli to the back or side of the head (or ears), whereas the somatosensory stimuli in the present study were delivered to the participant's hand which was placed in rear space (though see Kóbor, Füredi, Kovács, Spence, & Vidnyánszky, 2006, for a study of tactile TOJs in front versus rear space). It will therefore be particularly important for future research to assess whether spatial influences on AS interactions are dependent on the particular body surface stimulated, rather than merely on the presentation of stimuli within rear peripersonal space. The possibility of such differences is supported on one level by the examination of the representation of the body surface within area CM (Fu et al., 2003). Fu et al. found that 78 percent of AS neurons within macaque CM responded to cutaneous stimulation of the head, neck, and hands, with the majority of these neurons having unilateral somatosensory RFs on the head and neck. That is, there was a comparatively higher representation of the head and neck than the hands or other body surfaces tested. However, any functional consequences of these differences in the body representation in area CM await further examination.

One possibility is that AS interactions may rely on the distance of the stimuli from the body and/or head, with interactions being stronger for personal than for peripersonal space, the former of which would more heavily rely on representations of the head and neck. In support of this view, Graziano et al. (1999) found that tri-modal ventral pre-motor neurons containing somatosensory RFs on the sides and back of the head only responded to auditory stimuli that were presented within 30 cm of the head. Psychophysical (Kitagawa et al., 2005) and neuropsychological (Farnè & Làdavas, 2002) studies have similarly shown that AS interaction effects were greater when the auditory stimuli were presented close to (i.e., 20 cm) rather than far from (i.e., 70 cm) the back of the participant's head. Therefore, it would be particularly interesting in future studies to investigate the impact of spatial distance between auditory and somatosensory stimuli, particularly within rear space. Addressing such issues will be important if researchers are to arrive at a better understanding of the functional importance of AS interactions in front/rear and near/space. On a related point, it will be important to determine to what extent AS interactions are coded in terms of the egocentric and/or external spatial position of the stimulated body surface, if we are to understand the role of spatial coordinates in multisensory interactions.

In summary, the present study shows facilitatory AS interactions for both frontal and rear space, regardless of the relative spatial alignment of the stimuli. The novelty of the present results is in the demonstration of multisensory enhancement in rear space. Our data highlight the need for further investigation of multisensory phenomena in this region of space that is often neglected in multisensory research. Finally, the present results provide insights with regard to the likely RF organization within area CM mediating these AS multisensory interactions in humans.

Acknowledgements

References

Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience*, *25*, 189–220.

Caclin, A., Soto-Faraco, S., Kingstone, A., & Spence, C. (2002). Tactile "capture" of audition. *Perception & Psychophysics*, *64*, 616–630.

Caetano, G., & Jousmaki, V. (2006). Evidence of vibrotactile input to human auditory cortex. *Neuroimage*, *29*, 15–28.

Calvert, G. A., Spence, C., & Stein, B. E. (Eds.). (2004). *The handbook of multisensory processes*. Cambridge, MA: MIT Press.

Eimer, M., Van Velzen, J., & Driver, J. (2002). Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, *14*, 254–271.

Farnè, A., & Làdavas, E. (2002). Auditory peripersonal space in humans. *Journal of Cognitive Neuroscience*, *14*, 1030–1043.

Forster, B., Cavina-Pratesi, C., Aglioti, S., & Berlucchi, G. (2002). Redundant target effect and intersensory facilitation from visual–tactile interactions in simple reaction time. *Experimental Brain Research*, *143*, 480–487.

Foxe, J. J., Morocz, I. A., Murray, M. M., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2000). Multisensory auditory–somatosensory interactions in early cortical processing revealed by high-density electrical mapping. *Cognitive Brain Research*, *10*, 77–83.

Foxe, J. J., Wylie, G. R., Martinez, A., Schroeder, C. E., Javitt, D. C., Guilfoyle, D., et al. (2002). Auditory–somatosensory multisensory processing in auditory association cortex: An fMRI study. *Journal of Neurophysiology*, *88*, 540–543.

Frens, M. A., Van Opstal, A. J., & Van der Willigen, R. F. (1995). Spatial and temporal factors determine auditory-visual interactions in human saccadic eye movements. *Perception & Psychophysics*, *57*, 802–816.

Fu, K. M. G., Johnston, T. A., Shah, A. S., Arnold, L., Smiley, J., Hackett, T. A., et al. (2003). Auditory cortical neurons respond to somatosensory stimulation. *Journal of Neuroscience*, *23*, 7510–7515.

Fu, K. M. G., Shah, A. S., O'Connell, M. N., McGinnis, T., Eckholdt, H., Lakatos, P., et al. (2004). Timing and laminar profile of eye-position effects on auditory responses in primate auditory cortex. *Journal of Neurophysiology*, *92*, 3522–3531.

Gobbelé, R., Schürmann, M., Forss, N., Juottonen, K., Buchner, H., & Hari, R. (2003). Activation of the human posterior and temporoparietal cortices during audiotactile interaction. *Neuroimage*, *20*, 503–511.

Gondan, M., Niederhaus, B., Rösler, F., & Röder, B. (2005). Multisensory processing in the redundant-target effect: A behavioral and event-related potential study. *Perception & Psychophysics*, *67*, 713–726.

Gonzalez Andino, S. L., Murray, M. M., Foxe, J. J., & de Peralta Menendez, R. G. (2005). How single-trial electrical neuroimaging contributes to multisensory research. *Experimental Brain Research*, *166*, 298–304.

Graziano, M. S. A., Reiss, L. A. J., & Gross, C. G. (1999). A neuronal representation of the location of nearby sounds. *Nature*, *397*, 428–430.

Guest, S., Catmur, C., Lloyd, D., & Spence, C. (2002). Audiotactile interactions in roughness perception. *Experimental Brain Research*, *146*, 161–171.

Harrington, L. K., & Peck, C. K. (1998). Spatial disparity affects visual-auditory interactions in human sensorimotor processing. *Experimental Brain Research*, *122*, 247–252.

Holmes, N. P., & Spence, C. (2005). Multisensory integration: Space, time, and superadditivity. *Current Biology*, *15*, R762–R764.

Hötting, K., Rösler, F., & Röder, B. (2003). Crossmodal and intermodal attention modulate event-related brain potentials to tactile and auditory stimuli. *Experimental Brain Research*, *148*, 26–37.

Jay, M. F., & Sparks, D. L. (1987). Sensorimotor integration in the primate superior colliculus. II. Coordinates of auditory signals. *Journal of Neurophysiology*, *57*, 35–55.

Jousmaki, V., & Hari, R. (1998). Parchment-skin illusion: Sound-biased touch. *Current Biology*, *8*, R190.

Kayser, C., Petkov, C. I., Augath, M., & Logothetis, N. K. (2005). Integration of touch and sound in auditory cortex. *Neuron*, *48*, 373–384.

Kitagawa, N., & Spence, C. (2006). Audiotactile multisensory interactions in information processing. *Japanese Psychological Research*, *48*, 158–173.

Kitagawa, N., Zampini, M., & Spence, C. (2005). Audiotactile interactions in near and far space. *Experimental Brain Research*, *166*, 528–537.

Kóbor, I., Füredi, L., Kovács, G., Spence, C., & Vidnyánszky, Z. (2006). Back-to-front: Improved tactile discrimination performance in the space you can't see. *Neuroscience Letters*, *400*, 163–167.

Kujala, T., Alho, K., Kekoni, J., Hamalainen, H., Reinikainen, K., Salonen, O., et al. (1995). Auditory and somatosensory event-related potentials in early blind humans. *Experimental Brain Research*, *104*, 519–526.

Lütkenhöner, B., Lammertmann, C., Simões, C., & Hari, R. (2002). Magnetoencephalographic correlates of audiotactile interaction. *Neuroimage*, *15*, 509–522.

Menning, H., Ackermann, H., Hertrich, I., & Mathiak, K. (2005). Spatial auditory attention is modulated by tactile priming. *Experimental Brain Research*, *164*, 41–47.

Meredith, M. A., Nemitz, J. W., & Stein, B. E. (1987). Determinants of multisensory integration in superior colliculus neurons. I. Temporal factors. *Journal of Neuroscience*, *7*, 3215–3229.

Miller, J. O. (1982). Divided attention: Evidence for coactivation with redundant signals. *Cognitive Psychology*, *14*, 247–279.

Molholm, S., Ritter, W., Murray, M. M., Javitt, D. C., Schroeder, C. E., & Foxe, J. J. (2002). Multisensory auditory–visual interactions during early sensory processing in humans: A high-density electrical mapping study. *Cognitive Brain Research*, *14*, 115–128.

Murray, M. M., Foxe, J. J., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001). Visuo-spatial neural response interactions in early visual cortical processing during a simple reaction time task: A high-density electrical mapping study. *Neuropsychologia*, *39*, 828–844.

Murray, M. M., Molholm, S., Michel, C. M., Heslenfeld, D. J., Ritter, W., Javitt, D. C., et al. (2005). Grabbing your ear: Auditory–somatosensory multisensory interactions in early sensory cortices are not constrained by stimulus alignment. *Cerebral Cortex*, *15*, 963–974.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

Ortigue, S., Jabaudon, D., Landis, T., Michel, C. M., Maravita, A., & Blanke, O. (2005). Preattentive interference between touch and audition: A case study on multisensory alloesthesia. *Neuroreport*, *16*, 865–868.

Raab, D. (1962). Statistical facilitation of simple reaction times. *Transactions of the New York Academy of Sciences*, *24*, 574–590.

Schroeder, C. E., Lindsley, R. W., Specht, C., Marcovici, A., Smiley, J. F., & Javitt, D. C. (2001). Somatosensory input to auditory association cortex in the macaque monkey. *Journal of Neurophysiology*, *85*, 1322–1327.

Schroeder, C. E., Smiley, J., Fu, K. M. G., McGinnis, T., O'Connell, M. N., & Hackett, T. A. (2003). Anatomical mechanisms and functional implications of multisensory convergence in early cortical processing. *International Journal of Psychoanalysis*, *50*, 5–18.

Schröger, E., & Widmann, A. (1998). Speeded responses to audiovisual signal changes result from bimodal integration. *Psychophysiology*, *35*, 755–759.

Schurmann, M., Caetano, G., Hlushchuk, Y., Jousmaki, V., & Hari, R. (2006). Touch activates human auditory cortex. *Neuroimage*, *30*, 1325–1331.

Soto-Faraco, S., Spence, C., & Kingstone, A. (2004). Congruency effects between auditory and tactile motion: Extending the phenomenon of crossmodal dynamic capture. *Cognitive, Affective, & Behavioral Neuroscience*, *4*, 208–217.

Spence, C., McDonald, J., & Driver, J. (2004). Exogenous spatial cuing studies of human crossmodal attention and multisensory integration. In C. Spence & J. Driver (Eds.), *Crossmodal space and crossmodal attention* (pp. 277–320). Oxford, UK: Oxford University Press.

Spence, C., Nicholls, M. E. R., Gillespie, N., & Driver, J. (1998). Cross-modal links in exogenous covert spatial orienting between touch, audition, and vision. *Perception & Psychophysics*, *60*, 544–557.

Spence, C., & Zampini, M. (2006). Auditory contribution to multisensory product perception. *Acta Acustica United with Acustica*, *92*, 1009–1025.

Stein, B. E., & Meredith, M. A. (1993). *The merging of the senses*. Cambridge, MA: MIT Press.

Stein, B. E., Meredith, M. A., Huneycutt, W. S., & McDade, L. (1989). Behavioral indices of multisensory integration: Orientation to visual cues is affected by auditory stimuli. *Journal of Cognitive Neuroscience*, *1*, 12–24.

Stein, B. E., Stanford, T. R., Wallace, M. T., Vaughan, W. J., & Jiang, W. (2004). Crossmodal spatial interactions in subcortical and cortical circuits. In C. Spence & J. Driver (Eds.), *Crossmodal space and crossmodal attention* (pp. 25–50). Oxford: Oxford University Press.

Tolias, A. S., Moore, T., Smirnakis, S. M., Tehovnik, E. J., Siapas, A. G., & Schiller, P. H. (2001). Eye movements modulate visual receptive fields of V4 neurons. *Neuron*, *29*, 757–767.

Turatto, M., Galfano, G., Bridgeman, B., & Umiltà, C. (2004). Space-independent modality-driven attentional capture in auditory, tactile and visual systems. *Experimental Brain Research*, *155*, 301–310.

Wallace, M. T., & Stein, B. E. (2007). Early experience determines how the senses will interact. *Journal of Neurophysiology*, *97*, 921–926.

Werner-Reiss, U., Kelly, K. A., Trause, A. S., Underhill, A. M., & Groh, J. M. (2003). Eye position affects activity in primary auditory cortex of primates. *Current Biology*, *13*, 554–562.

Woods, T. M., Lopez, S. E., Long, J. H., Rahman, J. E., & Recanzone, G. H. (2006). Effects of stimulus azimuth and intensity on the single neuron activity in the auditory cortex of the alert macaque monkey. *Journal of Neurophysiology*, *96*, 3323–3337.

Worgotter, F., & Eysel, U. T. (2000). Context, state and the receptive fields of striatal cortex cells. *Trends in Neuroscience*, *23*, 497–503.

Zampini, M., Brown, T., Shore, D. I., Maravita, A., Röder, B., & Spence, C. (2005). Audiotactile temporal order judgments. *Acta Psychologica*, *118*, 277–291.