Auditory–somatosensory multisensory interactions in humans: Dissociating detection and spatial discrimination

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ABSTRACT

Simple reaction times (RTs) to auditory–somatosensory (AS) multisensory stimuli are facilitated over their unisensory counterparts both when stimuli are delivered to the same location and when separated. In two experiments we addressed the possibility that top-down and/or task-related influences can dynamically impact the spatial representations mediating these effects and the extent to which multisensory facilitation will be observed. Participants performed a simple detection task in response to auditory, somatosensory, or simultaneous AS stimuli that in turn were either spatially aligned or misaligned by lateralizing the stimuli. Additionally, we also informed the participants that they would be retrogradely queried (one-third of trials) regarding the side where a given stimulus in a given sensory modality was presented. In this way, we sought to have participants attending to all possible spatial locations and sensory modalities, while nonetheless having them perform a simple detection task. Experiment 1 provided no cues prior to stimulus delivery. Experiment 2 included spatially uninformative cues (50% of trials). In both experiments, multisensory conditions significantly facilitated detection RTs with no evidence for differences according to spatial alignment (though general benefits of cuing were observed in Experiment 2). Facilitated detection occurs even when attending to spatial information. Performance with probes, quantified using sensitivity (d'), was impaired following multisensory trials in general and significantly more so following misaligned multisensory trials. This indicates that spatial information is not available, despite being task-relevant. The collective results support a model wherein early AS interactions may result in a loss of spatial acuity for unisensory information.

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1. Introduction

Multisensory research on the manner in which the brain combines information from the different sensory epithelia has led to a paradigm shift in models of sensory organization. Anatomical, physiological, and brain imaging data demonstrate multisensory operations at levels of the cortical hierarchy including primary cortices (Ghazanfar & Schroeder, 2006; Kayser & Logothetis, 2007; Schroeder & Foxe, 2005; Stein & Stanford, 2008; Wallace, Ramachandran, & Stein, 2004). This new perspective has increased interest in determining the precise circumstances when multisensory interactions and their behavioral consequences will and will not occur.

The case of AS interactions is illustrative of this paradigm shift. Humans and non-human primates exhibit non-linear neural response interactions within the initial processing stages (Foxe et al., 2000; Lakatos, Chen, O'Connell, Mills, & Schroeder, 2007; Murray et al., 2005; Schroeder et al., 2001) and involve belt regions of auditory cortex adjacent to core auditory cortices (Fu et al., 2003; Kayser, Petkov, Augath, & Logothetis, 2005; Murray et al., 2005; Schroeder et al., 2001, 2003; see also Cappe & Barone, 2005; Hackett et al., 2007; Smiley et al., 2007 for corresponding anatomic data). Most recently, it has been shown that non-linear neural response interactions observed in humans are linked to behavioral outcome, such that non-linear neural response interactions over the 40–85 ms post-stimulus period were linked with facilitating reaction times (Sperdin, Cappe, Foxe, & Murray, 2009, Sperdin, Cappe, & Murray, 2010a).

More generally, identifying the necessary circumstances for inducing facilitative interactions can in turn provide insights into the likely organization of inputs onto structures (i.e., populations of neurons in the case of non-invasive studies in humans) contributing to multisensory integration. Facilitative effects on RT speed have

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now been observed not only when the stimuli are presented to the same location in space, but also when the stimuli are separated in space. This is the case for left-right (Murray et al., 2005), front-back (Zampini, Torresan, Spence, & Murray, 2007), as well as near-far (Tajadura-Jiménez et al., 2009) spatial disparities (see also Gillmeister & Eimer, 2007; Yau, Olenczak, Dammann, & Bensmaia, 2009). Such findings have been used to generate hypotheses concerning the spatial representation of auditory and somatosensory information within regions and at latencies when the initial neural response interactions have been repeatedly observed.

The rationale is predicated on the so-called "spatial rule" of multisensory interactions, which stipulates that the receptive field organization of a neuron (or neural population) is a determining feature of multisensory interactions and their quality (Stein & Meredith, 1993). Based on this principle and the above findings, it has been hypothesized that the initial AS neural response interactions are occurring within brain regions whose neuronal population consists of large (potentially 360°; Recanzone, Engle, & Juarez-Salinas, 2010; Woods, Lopez, Long, Rahman, & Recanzone, 2006) auditory spatial representations and unilateral somatosensory (i.e. hand) representations. To the extent that this is indeed the case, then it would be inaccurate to interpret cases where spatially misaligned stimuli lead to significant RT facilitation as an example where the spatial rule of multisensory interactions does not apply (cf. Murray & Spierer, 2009 for discussion).

One line of support for the above hypothesis is that the current evidence strongly supports a model of unisensory auditory spatial encoding that is based on population-level responses, rather than spatial mapping at the level of individual neurons (e.g. Stecker, Harrington, & Middlebrooks, 2005; also Murray & Spierer, 2009 and Spierer et al., 2010 for reviews). Another line of support comes from neurophysiologic studies of AS neural response interactions between spatially aligned and misaligned stimuli (Fu et al., 2003; Murray et al., 2005; see also Lakatos et al., 2007 for data focusing on oscillatory activity). Specifically, Murray et al. (2005) performed source estimations of neural response interactions and showed effects within the left caudal auditory cortices when the somatosensory stimulus was to the right hand, irrespective of whether the sound was within the left or right hemispace (and vice versa). These kinds of results suggest that spatial information is not a determining factor in whether or not facilitative effects at a population level will be observed.

However, it is important to note that simple detection does not (forcibly) require spatial processing of the stimuli, even though the stimuli are unambiguous in terms of their localization. Tasks that have required spatial processing often observed effects that were limited to spatially aligned conditions (Kitagawa, Zampini, & Spence, 2005; Kitagawa & Spence, 2006; see also Làdavas, Pavani, & Farnè, 2001; Farnè & Làdavas, 2002; Làdavas & Farnè, 2004; Ortigue et al., 2005). These discrepancies may stem from the task requirements and/or the need for spatial processing. The present study therefore addressed this discrepancy and more generally the question of whether early and low-level AS interactions (indexed by facilitated RTs that have previously been observed despite wide spatial separations between stimuli and that have been directly linked to such neurophysiological effects; Murray et al., 2005; Sperdin et al., 2009) are impacted by top-down influences on spatial processing. To do this, we introduce a novel paradigm that retains a stimulus detection task, while also requiring the continuous allocation of spatial attention (though not to a specific location). Specifically, across 2 experiments we examined whether multisensory facilitation of RTs during the performance of a simple detection task is affected when participants also attend to the spatial position of the stimuli. To do this, we modified a simple detection task by inserting retrograde spatial probe trials. In this way, we sought to have participants selectively attending covertly to each spatial

location, while nonetheless having them perform a simple detection task irrespective of spatial information. Experiment 1 did not involve any cuing prior to presentation of the imperative stimulus, whereas Experiment 2 presented cues on 50% of trials. These cues only served to indicate to participants to attend to the stimuli. The cues were not informative about the spatial location or the particular sensory modality(ies) that would be presented. Nor were they predictive of the subsequent presentation of a retrograde probe. The inclusion of pre-trial cues allowed for the assessment of whether participants could successfully deploy their attention to the task/stimuli and thus modulate their performance either on the detection task and/or with the spatial probes.

With this design we sought to disambiguate between two competing hypotheses of multisensory interactions (as indexed by facilitated RTs). On the one hand, one might hypothesize that making the spatial location of stimuli task-relevant will impact detection RTs such that facilitation is limited to spatially aligned stimuli or modulated between aligned and misaligned conditions. Such a pattern would be consistent with the proposition that task influences can dynamically modulate cerebral spatial representations (cf. Murray et al., 2005 for discussion). For example, dynamic shifts in receptive fields have been observed in neurons within the superior colliculus (Jay & Sparks, 1987) and parietal cortex (Andersen & Buneo, 2002). More recently, it has been shown that individual neuron's receptive fields can exhibit multiple, spatially distributed "hot spots" that in turn can vary as a function of the presented stimulus modalities (Krueger, Royal, Fister, & Wallace, 2009). On the other hand, the hypothesis we outline above would stipulate that even when spatial processing of the stimuli is emphasized, RT facilitation will be observed both when stimuli are spatially aligned and misaligned. This is because early, low-level neural response interactions occur within brain regions that (1) themselves contain a large representation (likely 360°) of auditory space (the precise extent of somatosensory spatial representations and variability across the body surface is currently unresolved; see Fu et al., 2003; Kayser et al., 2005; Tajadura-Jiménez et al., 2009) and (2) exhibit interactions even under conditions of anesthesia or passive stimulus presentation.

2. Materials and methods

2.1. Experiment 1

2.1.1. Participants

Sixteen participants (9 women; 7 men) aged 22–36 years took part in the experiment (mean 30 years). They included four women. Fourteen of the subjects were right-handed (Oldfield, 1971). All reported normal hearing and touch with no previous history of neurological or psychiatric illnesses. Each subject provided written, informed consent to participate in the study. All the procedures were approved by the Ethics Committee of the Faculty of Biology and Medicine of the University of Lausanne, Switzerland and were performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

2.2. Apparatus and stimuli

Auditory stimuli were 100 ms complex tones (square waveform, 10 ms rise/fall envelope to minimize clicks; 44,100 Hz digitization) generated using Adobe Audition 1.0 (www.adobe.com). Each sound was presented via insert earphones (model ER-4P; www.etymotic.com) at 75 dB (measured using a CESVA SC-L sound pressure meter; www.cesva.com). Vibrotactile stimulation was delivered through 2 (left and right hand) Oticon bone conducting devices (100 Ω, Oticon Inc., Somerset, NJ) with a duration of 100 ms and a vibrating surface of 1.6 cm wide × 2.4 cm long, which were held between the participant's index finger and thumb.[2] Continuous white noise was

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[2] It should be noted that in this regard our spatially aligned condition entailed stimuli that were presented to different locales on the same side of the participant. As such, the stimuli were not spatially co-localized. However, prior neurophysiological (Foxe et al., 2002) and psychophysical (Tajadura-Jiménez et al., 2009) indicate that spatial co-localization is not necessary to differentiate effects of spatial alignment. Plus, Experiment 2 of the present study entailed co-localized stimuli and replicated the findings of Experiment 1.
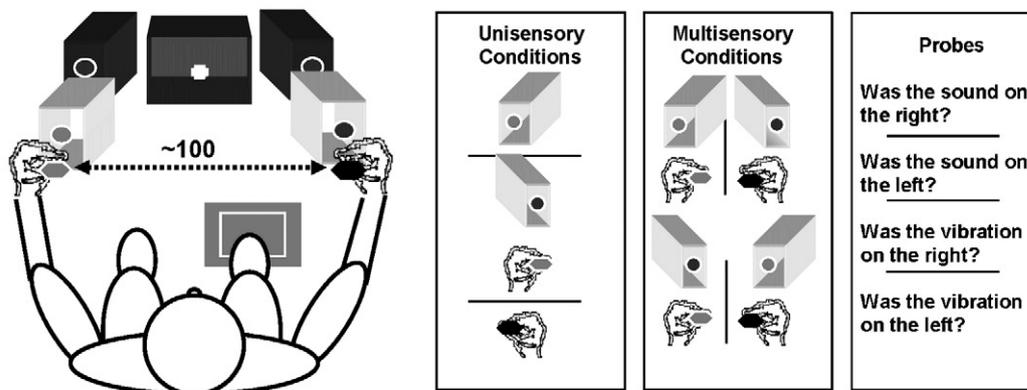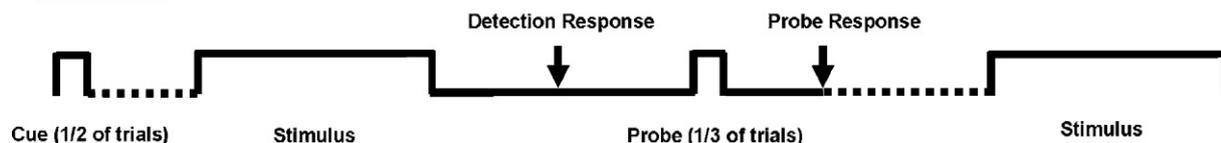
(a) Experiment 1

Stimuli
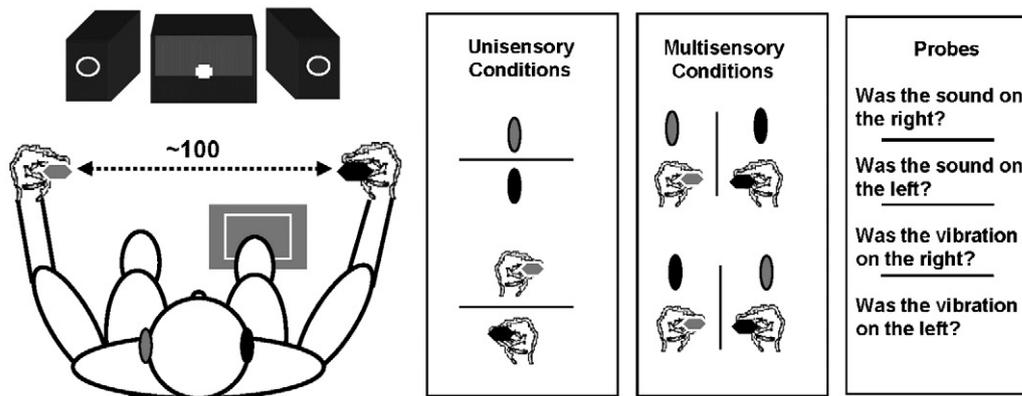
Trial Structure
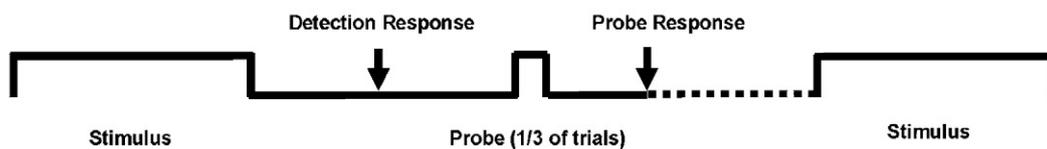
(b) Experiment 2

Stimuli

Trial Structure

Fig. 1. Experimental paradigm. (a) This panel illustrates the apparatus for stimulus delivery and response execution, as well as the posture of the participants in Experiment 1. The lower portion illustrates a typical trial structure. Stimuli were presented for 100 ms and participants then performed a detection response via a foot pedal under their right foot. On one-third of trials they were subsequently prompted with a probe inquiring about the spatial position of a particular sensory modality from the preceding trial. (b) This panel illustrates the apparatus and trial structure in Experiment 2.

played during the experiment to prevent subjects from hearing the sound produced by the bone conducting devices (see below). Behavioral data were collected throughout the length of the experiment while subjects sat in an electrically shielded and sound attenuated room. Stimulus delivery and response recording were controlled by E-Prime (Psychology Software Tools, Pittsburgh, PA; www.pstnet.com).

2.3. Procedure and task

Participants performed a simple detection task in response to auditory, somatosensory (vibrotactile stimulation of the left or right index finger and thumb), or simultaneous AS stimuli that in turn were either spatially aligned or misaligned

(e.g. auditory stimulation to the left and somatosensory stimulation to the right). The participants had to detect any stimulus through a foot pedal (right foot) while maintaining central fixation on a white cross presented in the middle of a black computer screen whilst attending to the spatial location of the stimuli (see Fig. 1a). Participants' arms were comfortably outstretched in front of them on armrests and were separated by ∼100° in azimuth.

In addition to the simple detection task, we also informed the participants that they would be queried from time to time (one-third of trials) as to whether or not a given stimulus in a given sensory modality had been presented to the left or right on the preceding trial. That is, on the probed trial, they had to indicate whether the sound or the vibration from the immediately preceding trial (that could be one of

the eight possible stimulus configurations) had been presented on the left or on the right side of space with respect to midline. Four possible probes were presented (i.e. referring to sound or vibration on the left or right) used for the eight conditions (four unisensory and four multisensory). Probes required positive and negative responses equally often, resulting in 16 total possible combinations with the stimulation trials. Probes following unisensory trials always queried the appropriate sensory modality (e.g. an auditory stimulus could only be followed by a probe about the position of a sound). Each of the eight stimulus configurations was randomly presented with equal frequency in blocks comprising 144 trials, and each of the four possible probes was also randomly interspersed (i.e. on 48 of the possible 144 detection trials). For trials without probes, the inter-stimulus interval varied from 1000 to 1500 ms in 100 ms steps that were equally distributed across the stimulus conditions. For those trials with probes, the interval between the stimulus and probe varied from 1000 to 1500 ms in 100 ms steps that were equally distributed across the conditions. The probe then remained on the computer screen for a total duration of 1500 ms irrespective of when the participant responded to the probe. The next trial began after an interval (with no stimuli on the screen) ranging from 1000 to 1500 ms in 100 ms steps equally distributed across conditions. Each participant completed 3 blocks of trials. Accuracy rates and RTs were measured for the detection portion, whereas only accuracy rates were measured for the probes. Only RTs in the range of 150–1000 ms were included in analyses. This resulted in the exclusion of on average less than 2% of trials (range 0.2–4.6%). As preliminary analyses revealed no effect or interaction involving side of stimulation, data were collapsed across left-sided and right-sided presentations for all analyses reported here.

It is worth noting at this point that retrograde rather than anterograde probes were used to maintain a simple detection paradigm on the one hand and also to require participants to attend to the spatial position of stimuli in each sensory modality on the other hand. Had anterograde probes been used, detection and discrimination processes would have been superimposed and we would not have obtained as 'pure' a measure of stimulus detection. The retrograde probing ensured that the detection task was kept constant, whilst continuously monitoring the spatial location of stimuli. In this way, we sought to have participants monitoring all spatial locations, while nonetheless having them perform a simple detection task irrespective of spatial information. The participants were instructed to respond as accurately and rapidly as possible without any feedback about the correctness of their responses.

2.4. Experiment 2

2.4.1. Participants

Eleven participants aged 22–31 years took part in the experiment (mean 27.5 years). They included 7 women. Nine of the 11 subjects were right-handed (Oldfield, 1971). All reported normal hearing and touch with no previous history of neurological or psychiatric illnesses. Ten of these subjects had participated in Experiment 1 at least 4 months beforehand. Each subject provided written, informed consent to participate in the study. All the procedures were approved by the Ethics Committee of the Faculty of Biology and Medicine of the University of Lausanne, Switzerland and were performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

2.4.2. Apparatus and stimuli

Auditory stimuli were 100 ms complex tones (square waveform, 10 ms rise/fall envelope to minimize clicks; 44,100 Hz digitization) generated using Adobe Audition 1.0 (www.adobe.com). Sounds were presented via loudspeakers located next to each hand (Bose Companion 2 Series II) at 75 dB (measured using a CESVA SC-L sound pressure meter located at the position of ear; www.cesva.com). Vibrotactile stimulation was delivered through 2 (left and right hand) Oticon bone conducting devices (100 Ω, Oticon Inc., Somerset, NJ) with a duration of 100 ms and a vibrating surface of 1.6 cm wide × 2.4 cm long, which were held between the participant's index finger and thumb. Therefore, multisensory stimuli were co-localized as well as co-lateralized when presented in an aligned configuration (cf. 2). As in Experiment 1, continuous white noise was played during the experiment to prevent subjects from hearing the sound produced by the bone conducting devices. Visual stimuli used for cuing were centrally presented white arrows (<>) that were immediately adjacent to the central fixation cross and appeared for 350 ms. The interval between a cue and stimulus varied between 900 and 1500 ms in steps of 100 ms equally distributed across trial types. Behavioral data were collected throughout the length the experiment while subjects sat in an electrically shielded and sound attenuated room. Stimulus delivery and response recording were controlled by E-Prime (Psychology Software Tools, Pittsburgh, PA; www.pstnet.com).

2.4.3. Procedure and task

Experiment 2 was identical to Experiment 1 in all respects, with the exception of the following points (Fig. 1b). First, sounds were presented here from loudspeakers rather than from earphones. This ensured co-localization of the sounds in the case of aligned trials. Second, visual cues were presented on 50% of trials, but were in no way informative of the lateralization of the stimuli or the particular sensory modality or modalities that would be presented. Subjects were explicitly instructed to attend to the spatial position of the stimuli on trials when the cue appeared. We would again emphasize that our interest was in maintaining a simple detection task.

Consequently, the cue was solely intended to prepare participants for the upcoming trial while having them attend to all potential locations where the stimuli could be presented. Third, in Experiment 2, participants completed 6 blocks of trials so as to have a sufficient number of cued and uncued trials for each condition and for all probes.
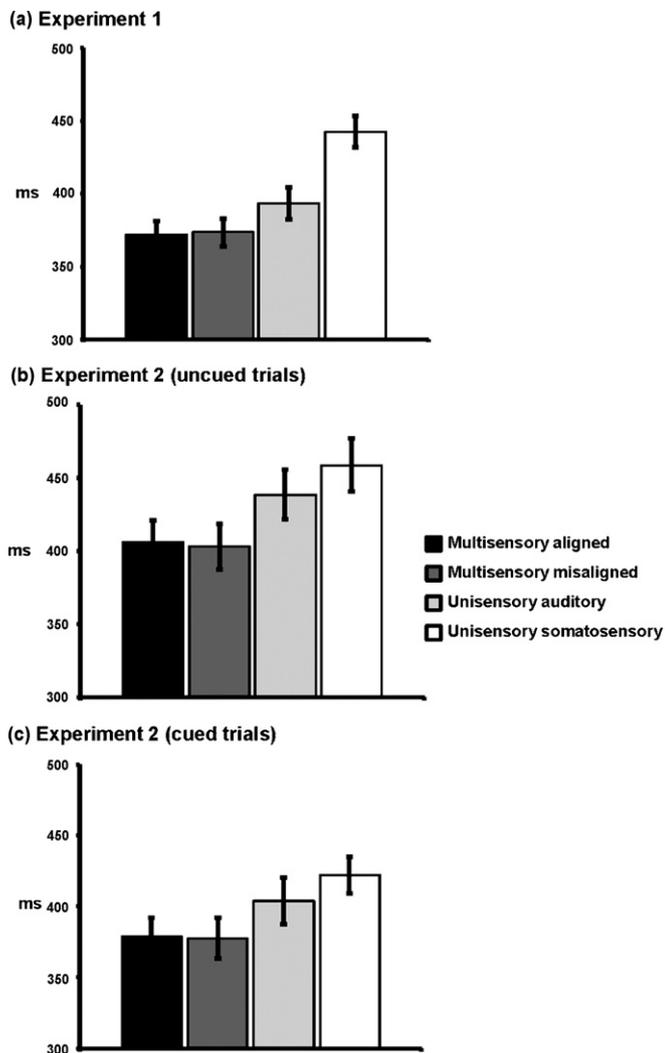
3. Results

3.1. Experiment 1

3.1.1. Detection

On average, subjects detected $97.9 \pm 0.6\%$ (mean ± s.e.m.) of auditory stimuli, $98.3 \pm 0.4\%$ of somatosensory stimuli, $98.1 \pm 0.4\%$ of spatially aligned multisensory stimulus pairs, and $97.7 \pm 0.5\%$ of spatially misaligned multisensory stimulus pairs. Detection rates were submitted to a repeated measures ANOVA using experimental condition as the within subjects factor with levels of auditory, somatosensory, multisensory aligned, and multisensory misaligned. Detection rates did not differ significantly across conditions ($p > 0.70$).

RT data were likewise submitted to a repeated measures ANOVA using experimental condition as the within subject factor with levels of auditory, somatosensory, multisensory aligned, and multisensory misaligned. There was a significant main effect of experimental condition ($F_{(3,13)} = 8.23$, $p < 0.0001$; $\eta_p^2 = 0.95$). Post hoc contrasts showed that RTs to multisensory stimuli were facilitated relative to either unisensory condition (all t-values > 4.60; p-values < 0.0001), with no difference between multisensory aligned and multisensory misaligned ($p = 0.56$; Fig. 2a). This pattern of results is indicative of a redundant signals effect (RSE) for both spatially aligned and misaligned AS stimuli, even when participants were retrogradely probed about the spatial location of stimuli (and therefore likely attended to their spatial position). Moreover, that RTs did not differ between spatially aligned and misaligned multisensory pairs provides no evidence for a spatial modulation of the RSE, in agreement with prior studies (Murray et al., 2005; Tajadura-Jiménez et al., 2009; Zampini et al., 2007)[3].

We also analyzed the RT data using Miller's race model inequality (Miller, 1982) to determine if the RT facilitation exceeded predictions based solely on probability summation. For this analysis, the probability distribution for each condition and participant were calculated (here using bins of 10% of the RT distribution across conditions for a given participant). This distribution for the multisensory aligned and misaligned conditions were compared to a modeled value for each of these conditions. The modeled value equals the summed probabilities from the constituent unisensory conditions minus their joint probability. When the actual probability is greater than the modeled value, the race model is violated and probability summation cannot account for the RSE obtained. The statistical robustness of this difference is in turn tested using a one-tailed paired t-test between the observed and modeled values. However, it should be noted that even when the race model is not violated, neural response interactions may likely be occurring (see e.g. Murray, Foxe, Higgins, Javitt, & Schroeder, 2001; Sperdin et al., 2009 for cases of such). In the present Experiment, only the misaligned multisensory trials resulted in significant violation of the race model inequality over the fastest 20% of the RT distribu-

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[3] It should be noted that the mean RTs here are akin to those observed by Murray et al (2005), but somewhat slower than those observed in either Zampini et al. (2007) or Tajadura-Jiménez et al. (2009). One possible explanation for this difference is that the foot was used for responding here, whereas the hand was used in Tajadura-Jimenez et al. Another difference is that the sounds were of lower intensity here and in Murray et al. than in Zampini et al. These things being said, further investigation is needed to explain variance in RTs across these studies. Nonetheless, and as is evident in the results, the pattern of findings is similar despite these paradigmatic differences.

(a) Experiment 1

(b) Experiment 2 (uncued trials)

- ■ Multisensory aligned
- ▨ Multisensory misaligned
- ☐ Unisensory auditory
- ☐ Unisensory somatosensory

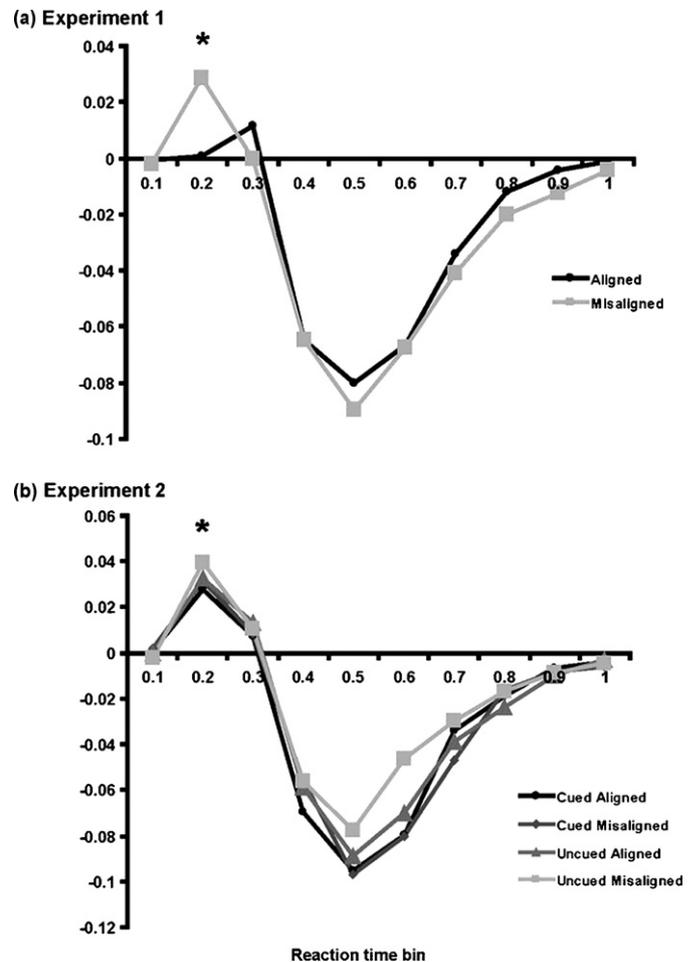**(c) Experiment 2 (cued trials)**

Fig. 2. Group average detection RTs (s.e.m. indicated). RTs to multisensory conditions were facilitated irrespectively of the spatial alignment between the auditory and somatosensory stimuli in Experiment 1 (panel a) as well as in Experiment 2 (panels b and c).

(a) Experiment 1

- —■— Aligned
- —■— Misaligned

(b) Experiment 2

- —◆— Cued Aligned
- —◆— Cued Misaligned
- —▲— Uncued Aligned
- —■— Uncued Misaligned

Reaction time bin

Fig. 3. Results of applying Miller's (1982) race model inequality to the cumulative probability distributions of the RT data. The difference between actual and modeled cumulative probability distributions is plotted as a function of the percentile of the RT distribution. (a) Results from Experiment 1 revealed a significant facilitation of RTs in excess of probability summation for misaligned multisensory trials. (b) Results from Experiment 2 revealed a significant facilitation of RTs in excess of probability summation for all conditions. In all panels asterisks indicate $p < 0.05$ (one-tailed t-test).

tion ($p < 0.01$; Fig. 3a). No significant violation was observed for the aligned multisensory trials, though we would note that 11 of the 16 participants exhibited violation at some point over the fastest 30% of the RT distribution. More germane, the finding that the misaligned condition produced significant violation of the race model provides one indication of the robustness of the RT facilitation even when stimuli are widely separated in space and when participants are (presumably) attending to the spatial position of individual sensory modalities.
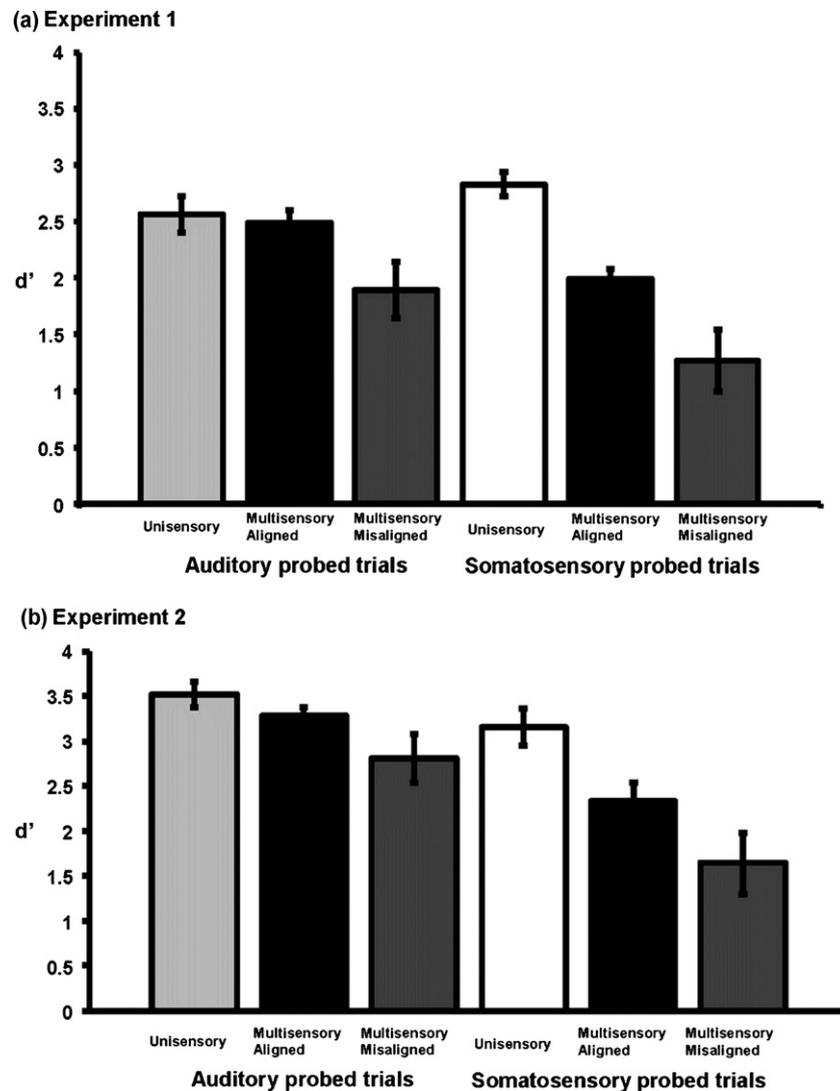
3.1.2. Spatial probes

Participants' performance with the spatial probes was generally highly accurate, indicative of the reliable attention to the spatial position of the stimuli. Hit rates for probes of sound lateralization were above 85% (range 86–92%), irrespective of the trial type (unisensory, multisensory aligned, and multisensory misaligned). By contrast, hit rates for probes of somatosensory lateralization were generally lower, ranging 66–80%, and varied as function of trial type. Accuracy data for the probes were analyzed according to signal detection theory (Green & Swets, 1966). Sensitivity (d') was calculated according to the following formula: $d' = z(H) - z(FA)$; where $z(H)$ and $z(FA)$ represent the transformation of the hit and false-alarm rates into z-scores (Macmillan &

Creelman, 1991). Hits were the stimuli correctly discriminated according to their spatial location (e.g. pressing the pedal to the probe "Was the sound on the right?" when the stimulus was a sound on the right, a multisensory stimulus with both the vibration and sound to the right, or a multisensory stimulus with the vibration on the left and the sound on the right). False alarms were the stimuli erroneously discriminated according to their actual spatial position (e.g. pressing the pedal to the probe "Was the sound on the right?" when the stimulus was a sound on the left). The results are displayed in Fig. 4a. Sensitivity in discriminating the spatial lateralization of stimuli were submitted to a 3×2 within subjects ANOVA, using trial type (unisensory, multisensory aligned, and multisensory misaligned) and probed modality (auditory, somatosensory) as factors. This analysis revealed a main effect of the trial type ($F_{(2,14)} = 25.19$, $p < 0.001$; $\eta_p^2 = 0.78$), a main effect of the probed modality ($F_{(1,15)} = 4.72$, $p < 0.05$; $\eta_p^2 = 0.24$), and an interaction between these factors ($F_{(2,14)} = 9.55$, $p = 0.002$; $\eta_p^2 = 0.58$). Follow-up contrasts were performed separately for each probed modality. In the case of probes of the lateralization of the sounds, d' was significantly lower for misaligned multisensory trials than for either aligned multisensory trials ($p < 0.05$) or unisensory trials ($p < 0.006$); the latter two of which did not significantly differ ($p > 0.65$). In the case of probes of the lateralization of

(a) Experiment 1

(b) Experiment 2

Fig. 4. Group-averaged (s.e.m. indicated) sensitivity (*d'*) with the spatial probes. (a) This panel displays results from Experiment 1. (b) This panel displays results from Experiment 2 after collapsed across cued and uncued trials (there was no main effect or cuing or interactions involving this term; see Section 3 for details). In both Experiments, sensitivity was impaired for probes following misaligned multisensory trials.

the vibro-tactile stimuli, *d'* was again significantly lower for misaligned multisensory trials than for either aligned multisensory trials ($p < 0.001$) or unisensory trials ($p < 0.008$); the latter two of which also significantly differed ($p < 0.001$). Thus, for both probed modalities sensitivity was significantly impaired following misaligned multisensory trials. However, because performance was also impaired for aligned multisensory trials (at least when the somatosensory modality was probed and albeit to a lesser degree than for misaligned multisensory trials) would argue against an explanation exclusively in terms of a response conflict due to there being two distinct spatial representations (i.e. one for each modality).

3.2. Experiment 2

3.2.1. Detection

When cued, subjects detected $99.1 \pm 0.5\%$ (mean ± s.e.m.) of auditory stimuli, $97.4 \pm 0.9\%$ of somatosensory stimuli, $99.6 \pm 0.2\%$ of spatially aligned multisensory stimulus pairs, and $99.5 \pm 0.2\%$ of spatially misaligned multisensory stimulus pairs. When not cued, subjects detected $98.7 \pm 0.6\%$ of auditory stimuli, $97.6 \pm 0.8\%$ of somatosensory stimuli, $99.5 \pm 0.3\%$ of spatially aligned mul-

tisensory stimulus pairs, and $99.5 \pm 0.2\%$ of spatially misaligned multisensory stimulus pairs. Detection rates were submitted to a repeated measures ANOVA using within subject factors of cuing (cued vs. uncued) and experimental condition (auditory, somatosensory, multisensory aligned, and multisensory misaligned). There was a main effect of condition ($F_{(3,8)} = 4.93$; $p = 0.032$; $\eta_p^2 = 0.65$) due to poorer performance on unisensory somatosensory trials relative to all other conditions. We would emphasize, however, that performance on unisensory trials was still nearly perfect ($97.5 \pm 0.8\%$). Likewise, there were no significant differences between any other conditions. Neither the main effect of cuing nor the interaction was significant (p-values > 0.65).

RT data were submitted to a repeated measures ANOVA as above, using within subject factors of cuing and experimental condition. There were significant main effects of cuing ($F_{(1,10)} = 26.48$, $p < 0.0001$; $\eta_p^2 = 0.73$) and experimental condition ($F_{(3,8)} = 93.57$, $p < 0.0001$; $\eta_p^2 = 0.97$), but no interaction between these factors ($p > 0.35$). Post hoc contrasts for cued and uncued trials, separately, showed that RTs to multisensory stimuli were facilitated relative to either unisensory condition (all t-values > 4.88; p-values < 0.001), with no difference between multisensory aligned and multisensory misaligned (p-values > 0.48; Fig. 3a). This pattern of results

is indicative of an RSE for both spatially aligned and misaligned AS stimuli, irrespective of whether or not the trial was cued and despite participants being informed that they would be retrogradely probed about the spatial location of stimuli. Moreover, that RTs did not differ between spatially aligned and misaligned multisensory pairs provides no evidence for a spatial modulation of the RSE, replicating our findings in Experiment 1 for both cued and uncued trials.

As in Experiment 1, we also analyzed the RT data using Miller's race model inequality (Miller, 1982) to determine if the RT facilitation exceeded predictions based solely on probability summation. Both aligned and misaligned conditions resulted RT facilitation exceeding probability summation over the fastest 10–30% of the RT distribution (Fig. 3b). This was the case both for cued and uncued trials. Race model violation was statistically evaluated with a paired *t*-test (one-tailed) between the actual and modeled probability distributions. For both the aligned and misaligned conditions as well as cued and uncued trials, the actual values were significantly higher than the modeled values for the bin spanning the fastest 10–20% of the RT distribution (all *p*-values < 0.023).

3.2.2. Spatial probes

Participants' performance with the spatial probes was generally highly accurate, indicative of the reliable attention to the spatial position of the stimuli. Hit rates for probes of sound lateralization were above 90% (range 91–98%) for both cued and uncued trials, irrespective of the trial type (unisensory, multisensory aligned, and multisensory misaligned). By contrast, hit rates for probes of somatosensory lateralization were generally lower, ranging 67–91%, and varied as function of trial type. Accuracy data for the probes were analyzed according to signal detection theory, as in Experiment 1. Mean d' values are displayed in Fig. 3b for both cued and uncued trials and were submitted to a $2 \times 3 \times 2$ within subjects ANOVA, using within subject factors of cuing (cued, uncued), trial type (unisensory, multisensory aligned, and multisensory misaligned) and probed modality (auditory, somatosensory). This analysis revealed main effects of trial type ($F_{(2,9)} = 7.20$, $p = 0.014$; $\eta_p^2 = 0.62$) and probed modality ($F_{(1,10)} = 25.57$, $p < 0.0001$; $\eta_p^2 = 0.72$), but no main effect of cuing ($p > 0.15$). There was also a significant interaction between trial type and probed modality ($F_{(2,9)} = 26.62$, $p < 0.001$; $\eta_p^2 = 0.86$). Data were therefore collapsed across cued and uncued trials, and one-way ANOVAs were conducted for each probed modality. When the lateralization of sounds was probed, there was no evidence for sensitivity differences across trial types ($p > 0.20$). By contrast, when the lateralization of touches was probed, there were significant differences in sensitivity across trial types ($F_{(2,9)} = 16.62$, $p < 0.001$; $\eta_p^2 = 0.79$) such that d' was significantly lower for misaligned multisensory trials than either aligned multisensory trials ($p = 0.021$) or unisensory trials ($p < 0.001$); with d' likewise being significantly lower for multisensory aligned than unisensory trials ($p = 0.022$). This pattern of results suggests that misaligned multisensory trials disrupt the ability to report the spatial location of somatosensory stimuli.

4. Discussion

The principal aim of the present study was to determine whether AS multisensory facilitation of RTs during the performance of a simple detection task is affected when the spatial position of the stimuli is also task-relevant. In particular, we assessed whether the facilitation of RTs when AS stimuli were spatially misaligned diminished or disappeared when performing a detection task that was followed by retrograde spatial probe trials. On those trials, participants had to indicate if during the immediately preceding event, the auditory or the somatosensory stimulus had been presented to the left or the right hemispace. This was motivated by the discrepancies observed across studies indicating that AS interactions are spatially modulated depending on factors such as task requirements and/or the need for spatial processing.

For the detection of stimuli, results from both experiments indicated that RTs were significantly and equally facilitated for both aligned and misaligned stimuli (see Fig. 2). That is, when the position and sensory modality of the stimuli were task-relevant a similar speeding up of RTs was obtained for the aligned and misaligned multisensory conditions relative to their constituent unisensory conditions. Moreover, no modulation was observed when comparing trials where stimuli were spatially misaligned vs. aligned. This is consistent with what has already been demonstrated in previous studies using simple detection tasks (Murray et al., 2005; Tajadura-Jiménez et al., 2009; Zampini et al., 2007). The novelty of the present results resides in the fact that this facilitation occurs despite the task-relevance of the lateralization of the stimuli (and by extension the likely engagement of spatial attention to successfully complete this task). Participants' high level of performance (vis à vis d') with the spatial probes provides a further indication that they indeed attended to the spatial position of the stimuli (though with some variation between audition and touch). However, the fact that d' with the spatial probes was generally lower following multisensory trials (both aligned and misaligned) than unisensory trials would suggest that AS interactions (both between aligned and misaligned combinations) transpiring between stimulus presentation and the presentation of a spatial probe interfere with the ability to report spatial information about one or the other sensory modalities.

Another consideration with regard to the pattern of detection RTs we obtained is that the equivalent facilitation under aligned and misaligned conditions can be construed as a null effect. In this way, our results are consistent with the proposition detailed by Kitagawa and Spence (2006) that interactions between the auditory and somatosensory modalities are inherently "less spatial" than other sensory combinations (though see Ho, Santangelo, & Spence, 2009 for data suggesting the importance of spatial alignment for AS stimuli to impact visual attention). Although we were able to replicate this pattern across both experiments, it could nonetheless be argued that the context of also performing a spatial discrimination task (on one-third of the trials) was simply insufficient to affect detection processes. It should be noted, however, that the requirements of the spatial discrimination task did indeed differentially affect performance with the probes themselves. Such being said, we cannot unequivocally refute the possibility that differences in detection RTs would have emerged had a more demanding spatial task been performed or had we presented somatosensory stimuli to other body surfaces where effects of spatial alignment on a pure detection task have indeed been observed (Tajadura-Jiménez et al., 2009). That is, the body surface stimulated might play a particularly prominent role in whether or not RTs are facilitated when AS stimuli are spatially aligned or misaligned (Tajadura-Jiménez et al., 2009; see also Làdavas et al., 2001 and Ortigue et al., 2005 for clinical evidence). These issues will require continued investigation. The relative sensitivity of stimulation of different body surfaces to the spatial alignment of co-presented sounds would be a non-invasive means of generating hypotheses concerning the likely specificity of anatomical projections into multisensory brain structures (cf. Fu et al., 2003; Kayser et al., 2005; Tajadura-Jiménez et al., 2009 for discussion as well as Sperdin, Cappe, & Murray, 2010b for preliminary event-related potential findings).

In prior work by our group, we proposed that spatial constraints on AS interactions might modulate dynamically either as a function of top-down or task-related influences (Murray et al., 2005; see also Royal, Carriere, & Wallace, 2009 and Krueger et al., 2009

for recent neurophysiologic evidence for dynamic receptive fields during multisensory integration). Under this framework top-down influences (i.e. awareness of the possibility of retrograde spatial probes) might serve to reconfigure (presumably early) brain mechanisms to emphasize spatial properties. Such a mechanism would likely involve dynamically modifying spatial representations at a population level; a notion that derives some support from studies within the visual system (e.g. Tolias et al., 2001; Worgotter & Eysel, 2000) and auditory system (e.g. Recanzone, 1998). From an ethological perspective, it is worth noting that the relationship of auditory and somatosensory inputs is frequently in flux; particularly those involving the limbs vs. the face/neck. That is, we constantly move our limbs relative to our body. For instance, one's left hand can operate entirely in right space to produce sounds there (Maravita, Spence, & Driver, 2003; Obayashi et al., 2001). In contrast to the possible influence of task demands, the present results show that RT facilitation with misaligned AS stimuli persists despite participants being cognizant of the task-relevance of the spatial position of stimuli in each sensory modality (see also Farnè, Dematte, & Làdavas, 2003 for related findings with visuo-tactile stimuli).

The above points notwithstanding, our results on the detection portion of the paradigm suggest that the task-relevance of spatial information is not the prominent factor in whether or not the facilitation of RTs will occur when AS stimuli are misaligned. Rather, AS stimulus detection would appear to be somewhat hermetic to these influences. This finding is in line with the current neuroimaging and neurophysiologic evidence in humans and non-human primates showing that early and low-level interactions can be observed not only when the animals/humans are awake and behaving (Beauchamp, Yasar, Frye, & Ro, 2008; Brett-Green, Miller, Gavin, & Davies, 2008; Gonzalez Andino, Murray, Foxe, & de Peralta Menendez, 2005; Murray et al., 2005; Sperdin et al., 2009) but also when stimuli are passively presented (Foxe et al., 2000, 2002; Fu et al., 2003; Schroeder et al., 2001, 2003) and when participants are anesthetized (Kayser et al., 2005). Such being said, however, there is also evidence that early interactions are directly relevant for performance outcome (Sperdin et al., 2009, 2010a). The immediate question that arises from the results from the detection portion of the paradigm is the qualitative nature of the representation of the stimuli; specifically whether the spatial location of the stimuli remains encoded and can still be discerned or if instead the stimuli have been fused into a representation that lacks information about the spatial origin of the constituent stimuli. Another possibility that our paradigm does not allow us to exclude is that participants remain aware of the fact that stimuli originated from different locations in the case of misaligned conditions, but were unable to reliably report which specific stimulus originated at which location (i.e. they became confused or the memory trace was too weak upon presentation of the spatial probe). Future extensions of this work will partially address this by also probing whether the stimuli (in the case of multisensory trials) were presented to the same or opposite sides. Such notwithstanding debriefings with the participants would suggest that they did not subjectively find the probes on the misaligned trials to be more difficult or confusing than any other condition.

Nonetheless, following the presentation of probes, identification of the spatial position of an immediately preceding event was impaired when stimuli where misaligned in space relative to unisensory or aligned multisensory trials. We observed a particular inability of our participants to correctly identify the spatial location of the unisensory component of multisensory events when these were misaligned in space. However, we would note that in some cases sensitivity was impaired for *both* types of multisensory trials though always to a greater extent on misaligned trials. Thus, in contrast to the pattern observed during stimulus detection, performance on spatial discrimination was influenced by the spatial alignment of the stimuli. This provides a level of support for our presumption that the task required subjects to attend to the spatial position of the stimuli. In this respect, the present findings with the spatial probe task are consistent with prior neuropsychological findings on localization tasks that showed impaired performance with spatially misaligned stimuli (Farnè & Làdavas, 2002; Farnè et al., 2003; Ortigue et al., 2005). However, in contrast to these clinical findings performance was often also impaired in the present study for probes following multisensory aligned stimuli relative to those following unisensory stimuli. In this regard, AS multisensory interactions in general would appear to disrupt (subsequent) spatial processing.

Other studies used a temporal order judgment task to render spatial information relevant (i.e. in contrast to a standard simple detection paradigm; Kitagawa et al., 2005; Zampini, Shore, & Spence, 2003; Zampini et al., 2005). However, these studies have generated conflicting results regarding whether performance is impaired by misaligned distracter stimuli. While the relative contribution of the precise body surface stimulated as well as of the location at which stimuli are presented remain to be elucidated, these data would suggest that spatially misaligned stimuli might impact performance more when spatial processes are required. Our data are in general keeping with this conclusion in that sensitivity was particularly impaired for probes following spatially misaligned stimuli. On the one hand, it may be the case (as suggested above) that the spatial information or 'tag' of the AS stimuli is not maintained between stimulus presentation and the execution of the spatial discrimination task. However, if this were the case, one expectation would be poor performance in general. However, sensitivity was nearly perfect for the unisensory and aligned multisensory trials. On the other hand, it may be the case that such spatial tags are more difficult to maintain in the spatially misaligned condition; a speculation that will require further experimental evidence. That is, participants might well be maintaining a spatial tag for both sensory modalities separately, and these later conflict upon presentation of the probe.

In some respects, our findings are similar to capture phenomena (e.g. Santangelo, Ho, & Spence, 2008). To date, there have been two investigations of AS capture (Caclin, Soto-Faraco, Kingstone, & Spence, 2002; Occelli, Spence, & Zampini, 2009; see also Ho et al., 2009 for the capacity of AS stimuli to capture attention during the completion of a demanding visual task). Using a psychophysical staircase paradigm, Caclin and colleagues examined if the perceived location of sounds (presented to the left or right) would be affected by a concurrently presented vibratory somatosensory stimulus delivered to the fingertips positioned a midline. Sounds were misperceived as shifted toward the midline when presented with vibrations. The authors proposed that their data are consistent with AS interactions occurring at a perceptual level and furthermore might be independent of the allocation of attention (i.e. participants were instructed to ignore the vibrations). A similar capture phenomenon could be at play in the present study and would appear to operate symmetrically (i.e. with vibrations capturing sounds and sounds capturing vibrations).

The present paradigm might likewise assist in better understanding the underlying perturbation(s) in cases of extinction and neglect. For example, Farnè, Làdavas and colleagues (Farnè & Làdavas, 2002; Farnè et al., 2003) demonstrated that a touch on the contralesional side of space can be extinguished by an auditory or visual stimulus on the opposite (ipsilesional) side of space. The prevailing explanation of multisensory extinction is that this auditory or visual stimulus activates a somatosensory representation on the ipsilesional side whose activity in turn competes with the actual somatosensory stimulus on the contralesional side. An alternative that would be supported by the present data is that there is a direct interaction between AS stimuli presented to differ-

ent sides of space. Completion of the present paradigm by patients with neglect/extinction might thus reveal the extent to which the underlying perturbations are perceptual vs. attentional. A related line of research in healthy controls has shown that when participants are asked to respond to both stimuli of a multisensory pair, they sometimes respond more to one sensory modality instead of the other and even report having perceived only one of the stimuli. One interpretation of this phenomenon – termed the Colavita effect (Colavita, 1974) – is that it is in many ways analogous to extinction phenomena (Spence, 2009). Interestingly, this effect has to date only been obtained with multisensory pairs that include visual stimuli, with no such effect obtained for AS combinations (Hecht & Reiner, 2009; though see Occelli, O'Brien, Spence, & Zampini, 2010 for very recent evidence of an AS Colavita effect with stimuli presented in rear space as well as for evidence for preferential detection of auditory vs. somatosensory stimuli, which is consistent with the generally higher d' values for probes on the lateralization of the auditory stimuli).

At a more general level with respect to AS interactions, our collective findings support the hypothesis that (early) AS interactions are mediated by brain regions containing large spatial representations (particularly in the case of the auditory modality). These interactions, which have been shown to be behaviorally relevant (at least for detection; Sperdin et al., 2009, 2010a) in turn engender facilitated detection RTs for both spatially aligned and misaligned pairings. The susceptibility of these interactions to (spatially uninformative) pre-stimulus cuing would appear to give rise to an unspecific facilitation of detection RTs irrespective of stimulus modality or spatial alignment with no evidence for an impact on retrograde spatial discrimination. By contrast, informing participants about the task-relevance of spatial information did not affect detection RTs but did affect retrograde spatial discrimination. While this might superficially appear contradictory, this pattern can be synthesized in the following manner. Following stimulus presentation AS interactions appear to be insensitive to left-right spatial alignment (Murray et al., 2005; though this remains to be systematically evaluated neurophysiologically as a function of body surface stimulated). This integrated representation in turn interferes with the ability to report the spatial position of either constituent unisensory stimulus. This is the case both when the stimuli are spatially aligned and all the more so when spatially misaligned. In this way, spatial information may become unavailable and/or less reliable, despite being task-relevant. The collective results support a model wherein early AS interactions may result in a loss of spatial acuity for unisensory information.

Acknowledgements

References

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

Beauchamp, M. S., Yasar, N. E., Frye, R. E., & Ro, T. (2008). Touch, sound and vision in human superior temporal sulcus. *Neuroimage*, 41, 1011–1020.

Brett-Green, B. A., Miller, L. J., Gavin, W. J., & Davies, P. L. (2008). Multisensory integration in children: a preliminary ERP study. *Brain Research*, 1242, 283–290.

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

Cappe, C., & Barone, P. (2005). Heteromodal connections supporting multisensory integration at low levels of cortical processing in the monkey. *European Journal of Neuroscience*, 22, 2886–2902.

Colavita, F. B. (1974). Human sensory dominance. *Perception & Psychophysics*, 16, 409–412.

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

Farnè, A., Dematte, M. L., & Làdavas, E. (2003). Beyond the window: Multisensory representation of peripersonal space across a transparent barrier. *International Journal of Psychophysiology*, 50, 51–61.

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. *Brain Research 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.

Fu, K. M., 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.

Ghazanfar, A. A., & Schroeder, C. E. (2006). Is neocortex essentially multisensory? *Trends in Cognitive Sciences*, 10, 278–285.

Gillmeister, H., & Eimer, M. (2007). Tactile enhancement of auditory detection and perceived loudness. *Brain Research*, 1160, 58–68.

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.

Green, D., & Swets, J. (1966). *Signal detection: Theory and psychophysics*. New York: Wiley.

Hackett, T. A., Smiley, J. F., Ulbert, I., Karmos, G., Lakatos, P., de la Mothe, L. A., et al. (2007). Sources of somatosensory input to the caudal belt areas of auditory cortex. *Perception*, 36, 1419–1430.

Hecht, D., & Reiner, M. (2009). Sensory dominance in combinations of audio, visual and haptic stimuli. *Experimental Brain Research*, 193, 307–314.

Ho, C., Santangelo, V., & Spence, C. (2009). Multisensory warning signals: When spatial correspondence matters. *Experimental Brain Research*, 195, 261–272.

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.

Kayser, C., & Logothetis, N. K. (2007). Do early sensory cortices integrate cross-modal information? *Brain Structure and Function*, 212, 121–132.

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 human 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.

Krueger, J., Royal, D. W., Fister, M. C., & Wallace, M. T. (2009). Spatial receptive field organization of multisensory neurons and its impact on multisensory interactions. *Hearing Research*, 258, 47–54.

Làdavas, E., & Farnè, A. (2004). Visuo-tactile representation of near-the-body space. *Journal of Physiology Paris*, 98, 161–170.

Làdavas, E., Pavani, F., & Farnè, A. (2001). Auditory peripersonal space in humans: A case of auditory-tactile extinction. *Neurocase*, 7, 97–103.

Lakatos, P., Chen, C. M., O'Connell, M. N., Mills, A., & Schroeder, C. E. (2007). Neuronal oscillations and multisensory interaction in primary auditory cortex. *Neuron*, 53, 279–292.

Macmillan, N., & Creelman, C. (1991). *Detection theory: A user's guide*. UK: Cambridge UP.

Maravita, A., Spence, C., & Driver, J. (2003). Multisensory integration and the body schema: Close to hand and within reach. *Current Biology*, 13, R531–539.

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

Murray, M. M., & Spierer, L. (2009). Auditory spatio-temporal brain dynamics and their consequences for multisensory interactions in humans. *Hearing Research*, 258, 121–133.

Murray, M. M., Foxe, J. J., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001). Visuo-spatial neural response interactions in early 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: Rapid auditory–somatosensory multisensory interactions in low-level sensory cortices are not constrained by stimulus alignment. *Cerebral Cortex*, 15, 963–974.

Obayashi, S., Suhara, T., Kawabe, K., Okauchi, T., Maeda, J., Akine, Y., et al. (2001). Functional brain mapping of monkey tool use. *Neuroimage*, 14, 853–861.

Occelli, V., Spence, C., & Zampini, M. (2009). The effect of sound intensity on the audiotactile crossmodal dynamic capture effect. *Experimental Brain Research*, 193, 409–419.

Occelli, V., O'Brien, J. H., Spence, C., & Zampini, M. (2010). Assessing the audiotactile Colavita effect in near and rear space. *Experimental Brain Research*, 203, 517–532.

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.

Recanzone, G. H. (1998). Rapidly induced auditory plasticity: The ventriloquism after effect. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 869–875.

Recanzone, G. H., Engle, J. R., & Juarez-Salinas, D. L. (2010). Spatial and temporal processing of single auditory cortical neurons and populations of neurons in the macaque monkey. *Hearing Research*,

Royal, D. W., Carriere, B. N., & Wallace, M. T. (2009). Spatiotemporal architecture of cortical receptive fields and its impact on multisensory interactions. *Experimental Brain Research*, 198, 127–136.

Santangelo, V., Ho, C., & Spence, C. (2008). Capturing spatial attention with multisensory cues. *Psychonomic Bulletin & Review*, 15, 398–403.

Schroeder, C. E., & Foxe, J. (2005). Multisensory contributions to low-level 'unisensory' processing. *Current Opinion in Neurobiology*, 15, 454–458.

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. 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 Psychophysiology*, 50, 5–17.

Smiley, J. F., Hackett, T. A., Ulbert, I., Karmas, G., Lakatos, P., Javitt, D. C., et al. (2007). Multisensory convergence in auditory cortex, I. Cortical connections of the caudal superior temporal plane in macaque monkeys. *Journal of Comparative Neurology*, 502, 894–923.

Spence, C. (2009). Explaining the Colavita visual dominance effect. *Progress in Brain Research*, 176, 245–258.

Sperdin, H. F., Cappe, C., Foxe, J. J., & Murray, M. M. (2009). Early, low-level auditory–somatosensory multisensory interactions impact reaction time speed. *Frontiers in Integrative Neuroscience*, 3, 2.

Sperdin, H. F., Cappe, C., & Murray, M. M. (2010a). The behavioral relevance of multisensory neural response interactions. *Frontiers in Neuroscience*, 4, 9–18.

Sperdin, H. F., Cappe, C., & Murray, M. M. (2010b). Mapping body surface and the spatial co-localization of sounds in auditory–somatosensory multisensory interactions. In *International multisensory research forum, 11th annual meeting*.

Spierer, L., De Lucia, M., Bernasconi, F., Grivel, J., Bourquin, N. M., Clarke, S., et al. (2010). Learning-induced plasticity in human audition: Objects, time, and space. *Hearing Research*, doi:10.1016/j.heares.2010.03.086

Stecker, G. C., Harrington, I. A., & Middlebrooks, J. C. (2005). Location coding by opponent neural populations in the auditory cortex. *PLoS Biol.*, 3, e78.

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

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: Current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, 9, 255–266.

Tajadura-Jiménez, A., Kitagawa, N., Valjamae, A., Zampini, M., Murray, M. M., & Spence, C. (2009). Auditory–somatosensory multisensory interactions are spatially modulated by stimulated body surface and acoustic spectra. *Neuropsychologia*, 47, 195–203.

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.

Wallace, M. T., Ramachandran, R., & Stein, B. E. (2004). A revised view of sensory cortical parcellation. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 2167–2172.

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 Neurosciences*, 23, 497–503.

Yau, J. M., Olenczak, J. B., Dammann, J. F., & Bensmaia, S. J. (2009). Temporal frequency channels are linked across audition and touch. *Current Biology*, 19, 561–566.

Zampini, M., Shore, D. I., & Spence, C. (2003). Audiovisual temporal order judgments. *Experimental Brain Research*, 152, 198–210.

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

Zampini, M., Torresan, D., Spence, C., & Murray, M. M. (2007). Auditory–somatosensory multisensory interactions in front and rear space. *Neuropsychologia*, 45, 1869–1877.