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RESEARCH****Research Report****Temporo-nasal asymmetry in multisensory integration mediated by the Superior Colliculus**Caterina Bertini<sup>a,b</sup>, Fabrizio Leo<sup>a,b</sup>, Elisabetta Làdavas<sup>a,b,\*</sup><sup>a</sup>Dipartimento di Psicologia, Università di Bologna, Bologna, Italy<sup>b</sup>Centro Studi e Ricerche in Neuroscienze Cognitive, Polo Didattico e Scientifico, Cesena, Italy

## ARTICLE INFO

## Article history:

Accepted 19 March 2008

## Keywords:

Temporo-nasal asymmetry

Multisensory integration

Superior Colliculus

Visual orienting response

## ABSTRACT

Temporo-nasal asymmetry in visual responses has been observed in many behavioural studies. These observations have typically been attributed to the anatomical asymmetry of fibres projecting to the Superior Colliculus (SC), even though this attribution is debated. The present study investigates temporo-nasal asymmetry in multisensory integration, and, by exploiting the absence of S-cone input to the SC, measures a behavioural response dependent strictly on the activity of the SC itself. We used a redundant signal paradigm for simple reaction times, with visual stimuli (red or purple) presented in either the temporal or the nasal hemifield. Participants responded more quickly to concurrent audio-visual (AV) stimuli than to either an auditory or a visual stimulus alone, an established phenomenon known as the Redundant Target Effect (RTE). The nature of this effect was dependent on the colour of the visual stimuli, suggesting its modulation by collicular circuits. When spatially-coincident audio-visual stimuli were visible to the SC (i.e. red stimuli), the RTE depended on a neural coactivation mechanism, suggesting an integration of multisensory information. When using stimuli invisible to the SC (i.e. purple stimuli), the RTE depended only on a simple statistical facilitation effect, in which the two sensory stimuli were processed by independent channels. Finally, we demonstrate that the multisensory integration effect was stronger for stimuli presented to the temporal hemifield than to the nasal hemifield. Taken together, these findings suggested that multisensory stimulation can be differentially effective depending on specific stimulus parameters.

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**1. Introduction**

The existence of a biased representation favouring the temporal hemifield in the Superior Colliculus (SC) has been investigated in several behavioural studies and its functional relevance in humans has been shown in a wide range of visual orienting behaviours. For instance, adult subjects show a bias to saccade towards temporal visual stimuli under conditions of

bilateral, simultaneous stimulation (Posner and Cohen, 1980). Additionally, a temporo-nasal asymmetry has been found in covert orienting behaviour (Rafal et al., 1991), in unconscious priming effects (Ansorge, 2003) and in more subtle measures such as saccadic latencies (Kristjansson et al., 2004). A pronounced bias in orienting saccades towards stimuli in the temporal hemifield versus the nasal hemifield has also been shown in newborns (Lewis and Maurer, 1992). Moreover,

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Abbreviations: A, Auditory; V, Visual; AV, Audio-visual; SP, Same Position; DP, Different Position; T, Temporal; N, Nasal; RMI, Race Model Inequality

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doi:10.1016/j.brainres.2008.03.087

hemianopic patients demonstrate a temporal hemifield advantage in both the oculomotor distractor effect (Rafal et al., 1990) and in a forced choice localization paradigm (Dodds et al., 2002). Such advantages in the representation of the temporal hemifield have been attributed to an asymmetry in projections from the hemiretinae to the Superior Colliculus; this anatomical argument is based on the observation that the behavioural asymmetries are present only in subjects whose retinotectal pathways are fully functional, but whose geniculostriate pathways are either not yet mature, as in infants (Johnson, 1990), or are disrupted, as in hemianopic patients.

Neuroanatomical studies on cats support this anatomical account; it has been shown that the nasal hemiretina (processing the temporal hemifield) has a stronger direct input to the Superior Colliculus than the temporal hemiretina (processing the nasal hemifield) (Sherman, 1974). However, in monkeys, the presence of this asymmetry exclusively in retinotectal projections has been questioned (Hubel et al., 1975): in a study on the primate visual system, this temporo-nasal asymmetry has been observed for both the projections from the retina to the Superior Colliculus and from the retina to the dLGN (Williams et al., 1995).

Recently, an fMRI study (Sylvester et al., 2007) testing this asymmetry directly in the human brain revealed a stronger activation of the SC in response to stimuli presented in the temporal hemifield than in the nasal hemifield, whereas no differential activity was observed in the lateral geniculate nucleus (LGN) or in the retinotopic cortical areas V1 and V3. Although these results do not distinguish between structural asymmetries (i.e. more neurons responding to temporal stimuli) and functional ones (i.e. larger gain associated with responses to temporal stimuli), they constitute a direct physiological demonstration of the neural correlates of characteristic behavioural temporo-nasal asymmetries.

The aim of the present study is to investigate the properties of the collicular temporo-nasal asymmetry by using a new behavioural method that directly tests a Superior Colliculus dependent response, namely multisensory integration. The role of SC in mediating multisensory integration has been extensively investigated in animals using neurophysiological recordings (Stein and Meredith, 1993). These studies showed that multisensory neurons in the deep layers of the SC typically have spatially-coincident receptive fields, and that they exhibit multisensory response enhancement (i.e. the multisensory response exceeds the most effective unisensory component response) to multimodal stimulation delivered in close spatial and temporal proximity (Stein and Meredith, 1993; Wallace et al., 1992).

To provide evidence of temporo-nasal asymmetry in multisensory integration, we exploited the fact that neurophysiological studies have consistently reported the lack of retinal input to the SC from short-wave sensitive S-cones (de Monasterio, 1978; Marrocco and Li, 1977; Schiller and Malpeli, 1977; Sumner et al., 2002).

The argument that the SC receives no S-cone input is bolstered by evidence that S-cones signals reach the koniocellular layers of the lateral geniculate nucleus, from where they project to layers 2 and 3 of the striate cortex (Dacey and Lee, 1994; White et al., 1998). Moreover, S-cones stimuli are invisible to the magnocellular pathway, which rules out the possibility of feedback projections running from the visual cortex to the SC.

A recent study by Leo et al. (2007) took advantage of the Superior Colliculus' insensitivity to S-cone activity in order to demonstrate the pivotal role of the SC in mediating multisensory integration when a spatial orienting response is required. In a redundant signal paradigm for simple reaction time, the researchers presented peripheral monochromatic red (i.e. long-wavelength stimulus, visible to the SC) or purple (i.e. short-wavelength S-cone dependent stimulus, invisible to the SC) visual stimuli with concurrent acoustic stimuli in either the same or different locations within the visual field. Results provided evidence that RTs to spatially-coincident audio-visual (AV) stimuli were significantly faster than RTs to spatially-disparate AV stimuli when red stimuli were used, but not when purple stimuli were presented. Moreover, a second analysis based on Miller's race inequality model (RMI; Miller, 1982) showed that the RTs to red (but not purple) spatially-coincident AV stimuli could be ascribed to a neural coactivation mechanism, suggesting in this way a multisensory integration effect. In other words, the effect could not be explained exclusively as a statistical facilitation<sup>1</sup>.

Given that multisensory spatial integration requires the activation of the retinotectal pathway, different behavioural effects should be expected when presenting stimuli in the temporal hemifield than in the nasal, a result of the temporo-nasal asymmetry present in the SC. To test this hypothesis, subjects were presented with peripheral red (i.e. visible to the SC) or purple (i.e. invisible to the SC) visual stimuli, either with or without a spatial disparity to concurrent auditory stimuli, in a redundant signal paradigm for simple reaction time. Subjects performed the task monocularly, which created a simple way to isolate the temporal and nasal hemifields: when patching a single eye, the contralateral hemifield becomes temporal and the ipsilateral field nasal. As predicted by Leo et al.'s study, an effect of spatial congruency (RTs shorter to spatially-coincident AV stimuli than to spatially-disparate AV stimuli) was expected only when red stimuli were presented; moreover, multisensory spatial integration (i.e. violation of the race model) should occur only with AV spatially-coincident stimuli visible to the SC. In accordance with temporo-nasal asymmetry, the magnitude of the violation of the race model was expected to be stronger for stimuli presented in the temporal rather than in the nasal hemifield. Conversely, no effect of spatial congruency was expected when purple stimuli (i.e. invisible to the SC) were presented.

## 2. Results

Participants responded to 1% of catch trials. RTs faster than 140 ms and slower than 650 ms were considered anticipations

<sup>1</sup> Note: To qualify the nature of the RTE (Redundant Target Effect: RTs to bi-sensory stimuli are faster, on average, than responses to unisensory ones; Todd, 1912), Miller (Miller, 1982) devised a mathematical method (race inequality test) that, using the cumulative frequency distribution (CFD) of RTs in the single versus double-target condition, sets an upper limit for the CDF when redundant target are presented (Miller, 1982, 1986):  $p(t < t_0 | AV) \leq p(t < t_0 | A) + p(t < t_0 | V)$ . If this limit is violated, then a statistical facilitation is no longer tenable, and the RTE can be attributed to a neural coactivation mechanism.

**Table 1 – Redundancy gain (RG)**

Red				Purple			
Stimulus	M	SD	RG	Stimulus	M	SD	RG
T V	335	36		T V	343	29	
N V	335	31		N V	346	30	
T A	304	76					
N A	308	79					
T SP-AV	259	36	62	T SP-AV	265	39	60
N SP-AV	260	37	59	N SP-AV	267	40	58
T DP-AV	267	39	52	T DP-AV	269	41	55
N DP-AV	267	40	55	N DP-AV	269	40	58

Mean RTs (M) and standard deviations (SD) in milliseconds for each stimulation condition, separately for the red visual stimulus and purple visual stimulus. RG is the difference between mean RTs in unimodal conditions and mean RTs in bimodal conditions. Auditory stimuli are labelled as temporal (T) and nasal (N): when subjects perform the task with the right eye patched, temporal auditory (TA) refers to an auditory stimulus presented in the left hemifield, whereas nasal auditory (NA) refers to an auditory stimulus presented in the right hemifield. On the contrary, when subjects perform the task with the left eye patched, temporal auditory (TA) refers to an auditory stimulus presented in the right hemifield, whereas nasal auditory (NA) refers to an auditory stimuli presented in the left hemifield. Note that the same RT data from unisensory auditory (T A and N A) conditions were used to calculate RG for red and purple visual stimuli. Abbreviations: T V=temporal visual, N V=nasal visual, T A=temporal auditory, N A=nasal auditory, T SP-AV=temporal spatially-coincident bimodal condition, N SP-AV=nasal spatially-coincident bimodal condition, T DP-AV=temporal spatially-disparate bimodal condition, N DP-AV=nasal spatially-disparate bimodal condition.

and delayed responses respectively, and were discarded (<1% of trials). Given that no differences between eyes were found in a preliminary analysis, reaction time data were analysed with a three-way ANOVA with Colour (red versus purple stimuli), Hemifield (temporal versus nasal) and Condition (unimodal visual, unimodal auditory, bimodal SP-AV, bimodal DP-AV) as within-subject factors.

Pairwise comparisons were conducted using the Newman-Keuls test. Overall, we found that responses to long-wavelength red stimuli (292 ms) were faster than responses to short-wavelength purple stimuli (296.4 ms), evidenced by the significant main effect of Colour [ $F(1,21)=16.7, p<.0006$ ].

We also found a significant main effect of Condition [ $F(3,63)=41.6, p<.000001$ ]. Responses to unimodal visual stimuli (340 ms) were significantly slower than responses to AV stimuli both in SP-AV condition (263 ms;  $p<.0002$ ) and in the DP-AV condition (268 ms;  $p<.0002$ ). Likewise, RTs in the unimodal auditory condition (306 ms) were significantly slower than RTs in both the SP-AV condition ( $p<.0002$ ) and DP-AV condition ( $p<.0002$ ). Finally, the redundancy gain (i.e., the RT difference between single and double stimulation) was similar in both hemifields for red and purple stimuli (see Table 1).

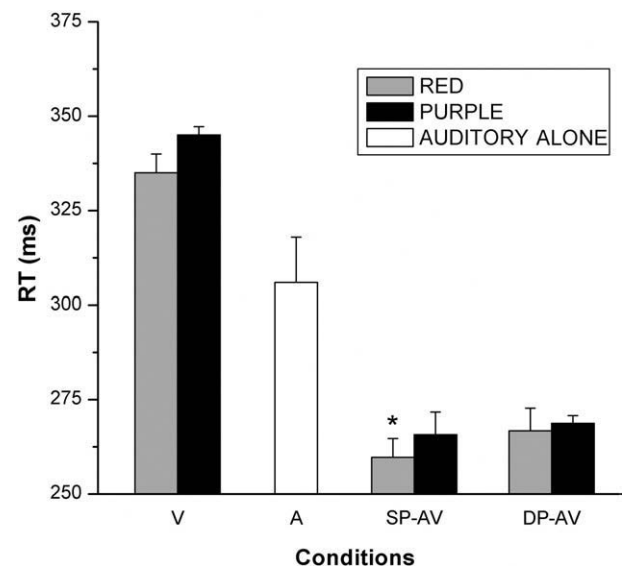
Moreover, we observed a significant interaction between Colour and Condition [ $F(3, 63)=7.8, p<.0002$ ]. That is, when the visual stimulus was red, RTs in the SP-AV condition were faster than RTs in the DP-AV condition (260 and 267 ms, respectively,  $p<.0002$ ), whereas, when the visual stimulus was purple, there was no significant difference between SP-AV (266 ms) and DP-AV (269 ms) conditions. In addition,

responses were significantly faster in the red SP-AV condition than in the purple SP-AV condition ( $p<.0003$ ) (see Fig. 1).

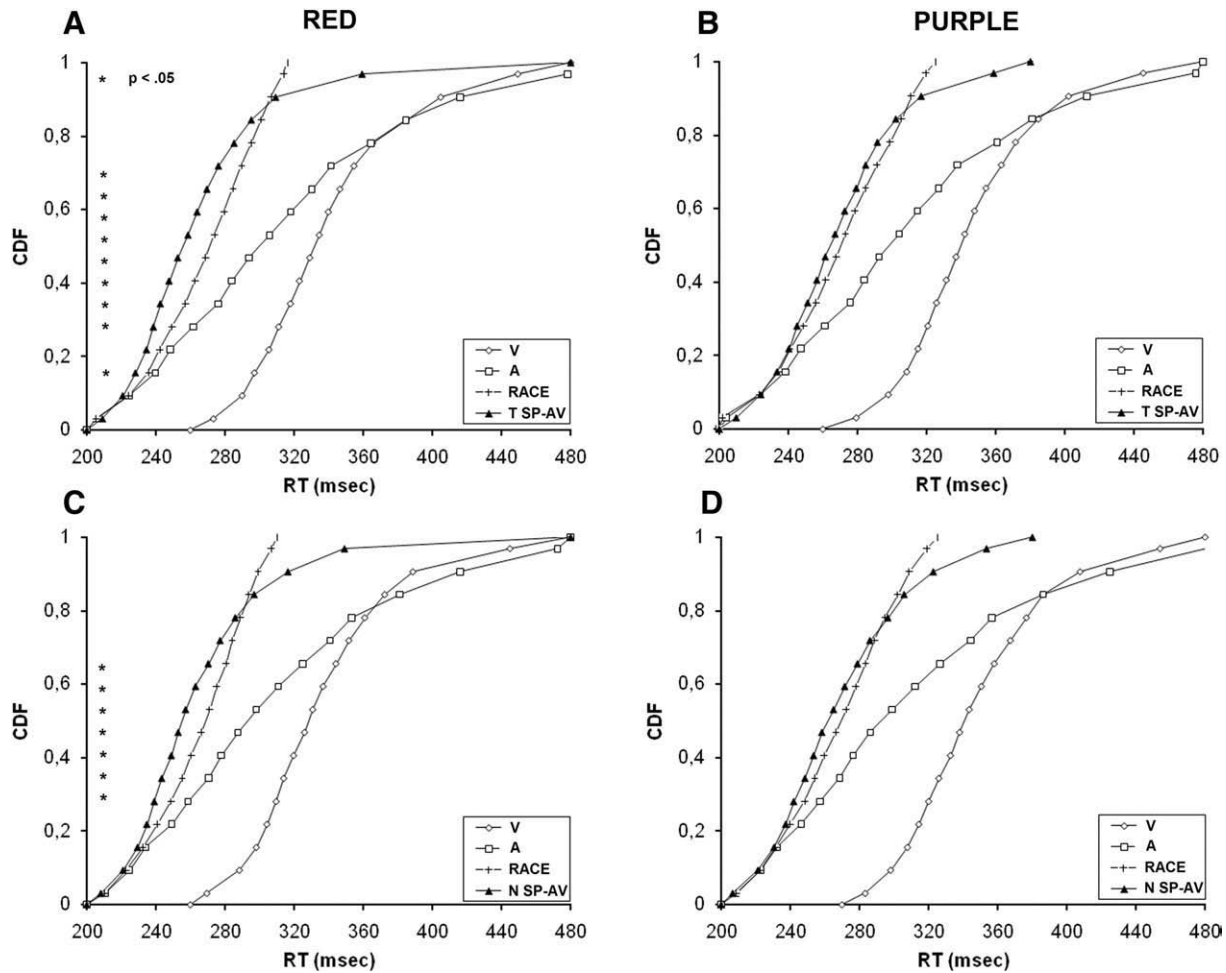
RT data were then analysed with Miller's race inequality test to determine whether the observed redundancy gains could be explained in terms of either a race or a neural coactivation model (Miller, 1982; Ulrich et al., 2007). A significant violation of race inequality was found only for red stimuli, in the spatially-coincident AV condition, in both the temporal and nasal hemifields (see Figs. 2 and 3). The grey rectangles in Fig. 3 indicate the percentiles in which the violation was significantly different from zero, as assessed by a t-test. Therefore, the RTE with red SP-AV stimuli violated the race inequality, and can therefore best be explained by neural coactivation. On the other hand, with the red DP-AV and with the purple (either SP-AV or DP-AV) stimuli, there was no race inequality violation, and therefore the RTE in these cases is best explained by statistical facilitation.

Given that a violation of the race inequality occurred with red SP-AV stimuli both in the temporal and nasal hemifields, we evaluated whether the magnitude of violation was significantly greater in the temporal compared to the nasal condition. To this aim, we computed the differences between the observed cumulative distribution functions (CDFs) and the CDFs predicted by the RMI for both the conditions (T SP-AV and N SP-AV), for all percentiles included in the violation areas, and then carried out a nonparametric inferential analysis (Wilcoxon matched pairs test). The result showed that the magnitude of the violation was reliably greater in the temporal SP-AV (median=14.63) than in the nasal SP-AV condition (median=10.83;  $z=2.80, p<.006$ ) (see Fig. 4).

Moreover, we computed the means of the differences between the observed and the predicted CDFs for each condition



**Fig. 1 – Mean reaction times.** Mean RTs (S.E.M. indicated) for each experimental condition (V=visual alone; A=auditory alone; SP-AV=same-position audio-visual condition; DP-AV=different-position audio-visual condition). Grey bars represent the conditions in which the visual stimulus was red; white bar represents the auditory alone condition; black bars represent the conditions in which the visual stimulus was purple.



**Fig. 2** – Cumulative reaction times. Observed cumulative reaction time (RT) distribution functions (CDFs) in the four spatially-coincident bimodal conditions and race model predictions from the respective RT CDFs to unimodal target stimuli. The two panels in the first column (A and C) show the conditions with red audio-visual stimuli presented in either the temporal (A) or nasal (C) visual field. The two panels in the second column (B and D) show the conditions with audio-visual purple visual stimuli in either the temporal (B) or nasal (D) visual field. Both the red spatially-coincident CDF presented in the temporal (T SP-AV) and nasal (N SP-AV) hemifield significantly outgrow the summed unimodal distributions, thus violating the race model. Asterisks are plotted for the percentiles where this violation is significant.

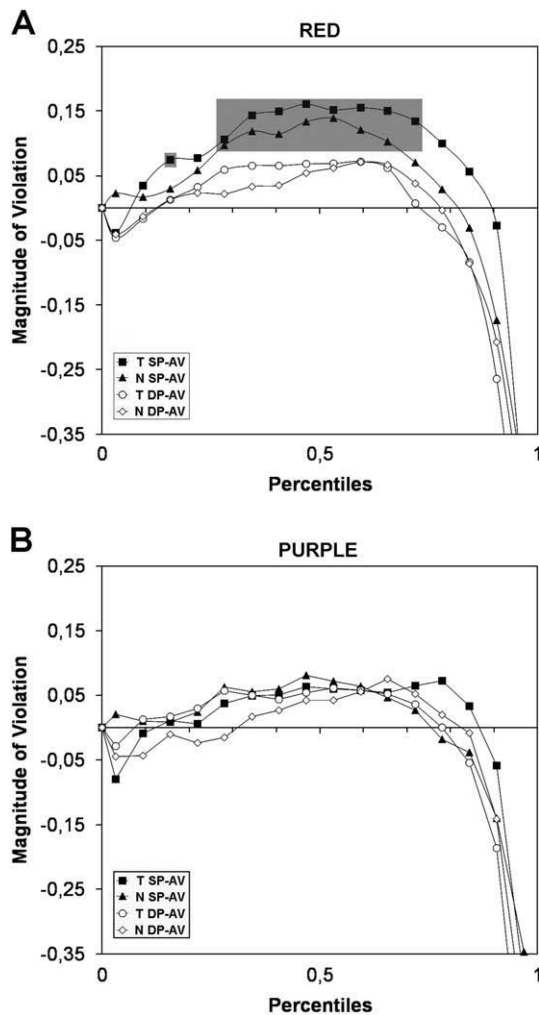
(T SP-AV and N SP-AV; 13 and 9.83, respectively). The ratio between the mean in the temporal condition and the mean in the nasal condition (1.32) was compared to the neurophysiologic naso-temporal ratio (1.57) reported by Williams et al. (1995). The result of a Fisher test (exact, 2-tail) demonstrated that the two ratios did not differ significantly ( $p = .403$ ).

### 3. Discussion

Neurophysiological evidence in animals and humans has consistently highlighted the critical involvement of the Superior Colliculus in visual orienting behaviour. Previous findings in monkeys have demonstrated that preparation of saccades and covert shifts of attention share a common neural network, in which the SC may play a pivotal role by determining orienting behaviour towards peripheral visual locations (Kustov and Robinson, 1996; Ignashchenkova et al., 2004).

A recent behavioural study of humans (Leo et al., 2007) provides further evidence of this collicular involvement in visual orienting responses. This study exploited the lack of S-cones inputs to the SC (Marrocco and Li, 1977; Schiller and Malpeli, 1977; de Monasterio, 1978; Sumner et al., 2002) and the relevance of this neural structure in the integration of different sensory inputs (Stein and Meredith, 1993). The results of the Leo et al.'s study showed that, when subjects were presented with peripheral visual stimuli, multisensory integration effects occurred only with stimuli visible to the SC; this important result suggests that the activity of the SC is absolutely necessary when a spatial orienting response is required.

The present study investigates temporo-nasal asymmetry in the SC, taking advantage of the behavioural technique proposed in Leo et al.'s study, which constitutes a direct way to study SC-mediated responses. To this end, a redundant target paradigm for simple reaction times was used, and AV stimuli were presented with either spatial coincidence or at a spatial disparity. The visual stimuli themselves could be either



**Fig. 3 – Violation of the race inequality.** Violation of the race inequality test for the four red (panel A) and purple (panel B) bimodal AV conditions of the experiment. The grey rectangles in the red condition mark the areas in which the violation is significantly different from zero (T SP-AV; N SP-AV), as assessed by one-sample t-test.

long-wavelength red stimuli (i.e. visible to the SC) or short-wavelength purple stimuli (i.e. invisible to the SC).

First, our results revealed an effect of spatial congruency on RTs depending on the colour of the visual stimulus: RTs to spatially-coincident AV stimuli were found to be significantly faster than RTs to spatially-disparate AV stimuli only with red visual stimuli (i.e. visible to the SC), but not when purple visual stimuli (i.e. invisible to the SC) were presented.

In order to disambiguate the mechanism underlying the reduction of RTs to double stimuli, data were analysed accordingly to Miller's race inequality test (Miller, 1982, 1986). Results showed a significant race model violation for spatially-coincident AV stimuli only when a red visual stimulus was used; the effect was present in both temporal and nasal hemifields. This significant violation, although it does not rule out the possibility of a probabilistic race between signals transmitted along different channels (statistical facilitation; Colonius and Diederich, 2006), suggests that the

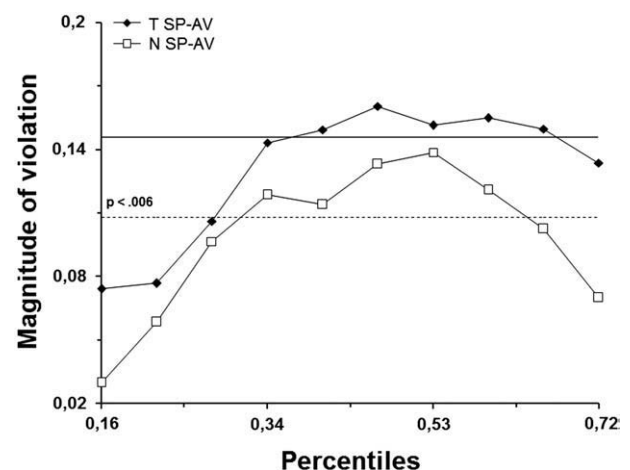
reduction of RTs to double stimuli may be due to a neural coactivation mechanism resulting from the convergence of the incoming signals onto one or more brain centres (multisensory integration).

Taken together, the present findings are consistent with the results presented in Leo et al.'s study and reveal the presence of a multisensory integration effect in a task requiring a visual orientation response, only when the visual information reaches the SC and when the different sensory modalities originate from the same position in the space.

To characterize the temporo-nasal asymmetry in multisensory integration, a further analysis on the magnitude of violation of the race model was carried out with the results obtained in the temporal and nasal conditions. This analysis demonstrated a significantly greater violation of the race inequality in the temporal hemifield than in the nasal hemifield when a red visual stimulus was presented with a concurrent acoustic stimulus in the same spatial position. Moreover, the ratio between the magnitude of the violation in both the conditions seems to reflect the ratio of the fibres projecting to the SC observed at neural level: an electrophysiological study examining nasal and temporal retinal ganglion cells, retrogradely labelled in the SC of four macaque monkeys, revealed a mean naso-temporal ratio in the collicular projection of 1.57 (Williams et al., 1995). The present study describes an asymmetry in multisensory effects that appears to be linearly related to the asymmetry of the afferent fibres to the SC.

These findings corroborate the notion that an anatomical bias favours the temporal hemifield in the SC. They are consistent with the results of a recent fMRI study revealing greater SC responses to visual stimuli in the temporal hemifield than in the nasal hemifield; no such bias was apparent in geniculostriate pathway structures such as LGN and cortical areas V1 and V3 (Sylvester et al., 2007).

The notion that the stimulation of the temporal hemifield leads to a greater multisensory response enhancement,



**Fig. 4 – Hemifield violation of the race inequality.** Comparison of the magnitude of violation of red temporal same-position audio-visual condition (T SP-AV) and red nasal same-position audio-visual condition (N SP-AV), for all percentiles included in the violation areas. Filled line represents the median of T SP-AV distribution. Dashed line represents the median of N SP-AV distribution.

comparing to the stimulation of the nasal hemifield, and the relevance of SC in visual orienting behaviour, suggest an adaptive function of this midbrain structure. Both the ability to integrate different sensory modalities into a unified multisensory map of the external environment, and the bias in orienting towards stimuli in the periphery of the visual field, might have evolved because of significant survival advantages in rapidly orienting towards salient peripheral stimuli.

The results of the present study have several operational implications. Recent clinical studies on hemianopic patients (Bolognini et al., 2005) have demonstrated that multisensory stimulation can systematically activate the SC and, therefore, can constitute a therapeutic tool in the recovery from spatial representational disorders. From this perspective, the observed temporo-nasal asymmetry lends support to the suggestion that stimulating the temporal hemifield should improve the therapeutic efficacy of rehabilitative treatments based on multisensory integration.

To sum up, the present study provides evidence of a temporo-nasal asymmetry in a multisensory integration effect mediated by the SC. By taking advantage of the absence of retinal input to the SC from short-wave sensitive S-cones, we have shown the presence of a multisensory spatial integration effect that occurs only with visual stimuli visible to the SC. In addition, we have demonstrated that this effect is stronger for stimuli presented to the temporal hemifield than to the nasal hemifield.

## 4. Experimental procedures

### 4.1. Participants

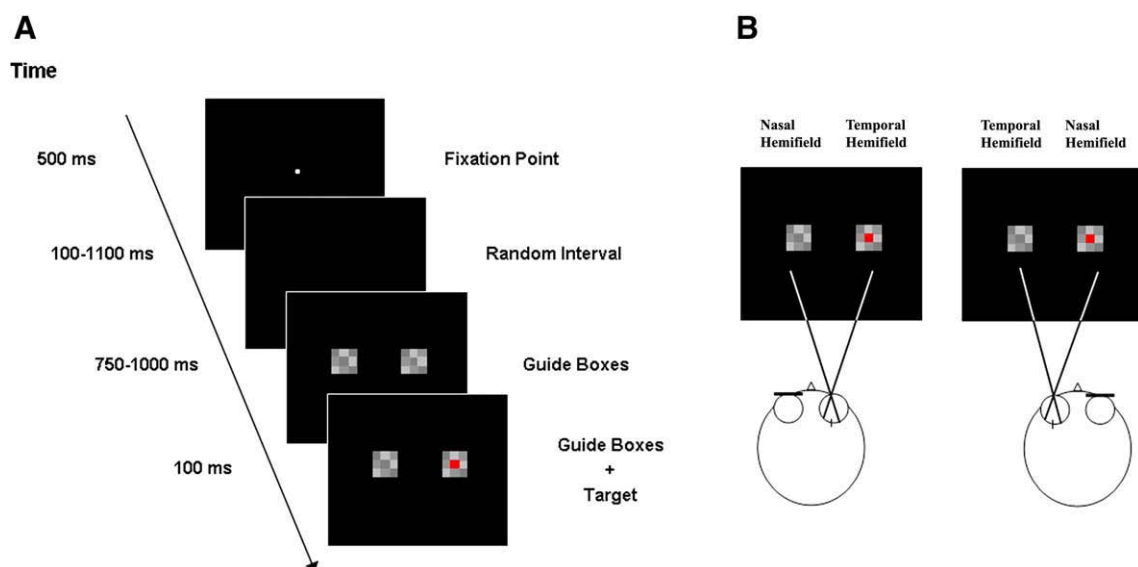
Eleven healthy subjects (age range: 21–31 years; three males and eight females) took part in the experiment. All had normal hearing and normal or corrected-to-normal vision and were

naive as to the purpose of the experiment. Participants received course credit for their participation and gave informed consent prior to beginning. The experimental procedures were approved by the Ethical Committee of the Department of Psychology, University of Bologna. The experiment was carried out according to the principles laid out in the 1964 Declaration of Helsinki.

### 4.2. Stimuli and procedures

Subjects sat in a completely dark room in front of a Samsung SyncMaster 153B 17 inch PC monitor at a distance of 57 cm. All stimuli were generated by a PC with MATLAB 6.1 and PSYCHOTOOLBOX 2.50 (Brainard, 1997; Pelli, 1997). Subjects were required to hold constant fixation on a central white dot against a black background ( $0.05 \text{ cd/m}^2$ ). The experimenter, standing behind the monitor and facing the subject, initialized each trial only when subject's eye were at fixation. In each trial (see Fig. 5A for the sequence of events in a trial) the fixation point lasted 500 ms and then, after an interval whose duration was randomised in a 100–1100 ms time window, two  $3^\circ \times 3^\circ$  square "guide boxes" were displayed  $6^\circ$  to the right and to the left of the fixation point with an exposure duration ranging between 750 and 1000 ms. Each box was made up of nine squares changing luminance every 67 ms to a value drawn randomly from the range  $4.05\text{--}6.75 \text{ cd/m}^2$ . This luminance noise ensured that the colour changes described below could be detected only by a chromatic channel (Birch et al., 1992; Leo et al., 2007; Mollon, 1982; Savazzi and Marzi, 2004; Sumner et al., 2002).

The visual stimuli were  $1^\circ \times 1^\circ$  squares randomly presented at the centre of one of the two guide boxes, in the last 100 ms of guide boxes' presentation. The visual stimuli could be either short-wavelength (purple; colorimetric values:  $x=0.1826$ ,  $y=0.0869$ ) or long-wavelength (red; colorimetric values:  $x=$



**Fig. 5 – Schematic diagram of the experimental setup. Panel A represents a schematic diagram of a typical trial in the experiment. Panel B shows schematic, top-down views of a subject, below the experimental displays. The visual target shown here is a long-wavelength stimulus (red). In the experiment, loudspeakers (not reported in the figure) were placed immediately below the guide boxes. Diagrams not to scale.**

0.6194,  $y=0.3455$ ). For all stimuli, exposure duration was 100 ms and the luminance was 5.4  $\text{cd/m}^2$ . Chromaticities and luminances were calculated from the spectra of each stimulus, which was measured directly with a Minolta chromameter CL-200.

The auditory stimuli comprised a 100 ms broadband burst of pure tones (2000 Hz), emitted by one of two piezoelectric loudspeakers (0.4 W, 8 W) located in front of the PC monitor, ~4 cm below the visual stimuli. The intensity level of the auditory stimuli was 66.3 dB SPL.

Subjects completed two different sessions varying by monocular condition (i.e. one with a patch covering the left eye and one with a patch covering the right eye). When patching the right eye, the left hemifield becomes temporal and the right nasal, whereas the reverse holds with the left eye patched instead (see Fig. 5B). Sessions' order was counter-balanced across subjects.

There were 14 randomly intermingled stimulus conditions:

- 1) unimodal auditory condition: the auditory stimulus was presented alone in the right or left hemifield;
- 2) unimodal visual condition: the visual stimulus (purple or red) was presented alone in the temporal (T V) or nasal (N V) hemifield;
- 3) same-position audio-visual condition: the visual (purple or red) presented in the temporal or nasal hemifield, T SP-AV and N SP-AV, respectively) and the auditory stimulus were presented simultaneously, in close spatial proximity;
- 4) different-position audio-visual condition: the visual (purple or red, presented in the temporal or nasal hemifield, T DP-AV and N DP-AV, respectively) and the auditory stimulus were presented simultaneously and in different positions (i.e., opposite hemifields).

Subjects were instructed to maintain fixation on the central white dot, and to respond by pressing the space bar of the keyboard with the index finger of the dominant hand as quickly as possible in response to any unimodal (visual or auditory) or bimodal stimulus.

A 5-min practice, run for each subject, preceded the experiment. Each session was subdivided into four blocks of trials with an overall number of 747 presentations for each participant. There were 40 trials for each type of stimulus condition, and 187 catch trials in which only the guide boxes were presented without the target stimuli. Catch trials were introduced to discourage the participant from responding to the guide box rather than to the target stimulus.

#### 4.3. Statistical analysis

For each subject, the average RTs were calculated and their distributions were recorded for each stimulus condition. To test for the presence of an RTE, planned comparisons between each of the unimodal stimulus conditions and the bimodal stimulus conditions were performed.

To determine if a statistical facilitation explanation for the RTE was tenable, or if a coactivation explanation of the RTE was necessary, Miller's test of the race model was implemented by using RMITest software (Miller, 1982; Ulrich et al., 2007). The program computes the estimated cumulative distribution functions (CDFs) of RT for each condition and the estimated

race model inequality bound. It also computes a t-test at each percentile to see whether the race model violation is statistically significant. The difference between the cumulative probability for the double stimuli and the sum of the cumulative probability for the single stimuli indicates the magnitude of violation.

#### Acknowledgments

This work was supported by grants from MURST to EL. We thank all the participants for their cooperation and Mario Mazzocchi for his helpful insights in statistical analysis.

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