

Hemispheric modulations of the attentional networks



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ABSTRACT

Although several recent studies investigated the hemispheric contributions to the attentional networks using the Attention Network Test (ANT), the role of the cerebral hemispheres in modulating the interaction among them remains unclear. In this study, two lateralized versions of this test (LANT) were used to investigate the effects on the attentional networks under different conflict conditions. One version, the LANTI-A, presented arrows as target and flankers, while the other version, the LANTI-F, had fruits as target and flankers. Data collected from forty-seven participants confirmed well-known results on the efficiency and interactions among the attentional networks. Further, a left visual field advantage was found when a target occurred in an unattended location (e.g. invalid trials), only with the LANTI-F, but not with LANTI-A. The present study adds more evidence to the hemispheric asymmetry of the orienting of attention, and further reveals patterns of interactions between the attentional networks and the visual fields across different conflicting conditions, underlying the dynamic control of attention in complex environments.

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1. Introduction

Every day, the human brain is constantly beset by incoming information from both sides of our visual fields, and attentional mechanisms are implemented to influence which information gains access to conscious awareness (Fan et al., 2009; Mackie, Van Dam, & Fan, 2013). Although humans are able to allocate attentional resources efficiently to both the left and right visual fields (hereafter LVF and RVF, respectively), the earliest evidence for the right hemisphere (RH) dominance for attention was found more than 30 years ago (Heilman & Van Den Abell, 1980; Kinsbourne, 1987; Mesulam, 1999). For example, spatial neglect is a neuropsychological syndrome characterized by a failure to perceive and respond to stimuli presented on the contra-lesional side of space, and this syndrome has been shown to be more severe and long-lasting following a right-sided brain lesion compared to a left-sided brain lesion (Bartolomeo, 2007; De Renzi, Gentilini, Faglioni, & Barbieri, 1989; Heilman & Van Den Abell, 1980; Riddoch & Humphreys, 1983). Further evidence of a RH dominance for visuospatial attention comes from studies on lateralized visuospatial attention bias in non-clinical samples, which has revealed a small

but systematic leftward bias, known as pseudoneglect, both in the line bisection task (i.e., marking the perceived center of a horizontal line) and the landmark task (i.e., judging whether a vertical line is to the left or right of the center of a horizontal line) (Bowers & Heilman, 1980; Brooks, Della Sala, & Darling, 2014).

A wealth of studies investigating the RH hemisphere specialization for attentional processing have used the cued response time paradigm (Posner, 1980), in which a visual target is preceded by the presentation of a cue that may (valid condition) or may not (invalid condition) indicate the exact position where the target will be presented. Typically, the cost of an invalid cue is reduced for targets appearing in the LVF (controlled by the RH) compared to targets presented in the RVF (controlled by the LH) (Evert, McGlinchey-Berroth, Verfaellie, & Milberg, 2003; Michael & Ojeda, 2005; Okada, Sato, & Toichi, 2006; Shenal, Hinze, & Heilman, 2012), although controversy exists (Chokron, Brickman, Wei, & Buchsbaum, 2000; Sosa, Teder-Sälejärvi, & McCourt, 2010). Support for the RH specialization for attentional processing also comes from several imaging studies (Corbetta & Shulman, 2011). In a pivotal PET study, Corbetta, Miezin, Shulman, and Petersen (1993) showed that changes in regional blood flow in right frontal and parietal regions were associated with movement of attention towards both visual fields, while the left parietal region was involved in shifts of attention towards the RVF only. Nowadays, many consider the RH to play a key role in the selective

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aspect of attention (De Schotten et al., 2011; Foxe, McCourt, & Javitt, 2003; Longo, Trippier, Vagnoni, & Lourenco, 2015; Ocklenburg, Güntürkün, & Beste, 2012; Rengachary, He, Shulman, & Corbetta, 2011; Shu, Liu, Duan, & Li, 2015; Shulman et al., 2010).

One view of attention conceptualizes it as the activity of a set of brain networks - alerting, orienting, and executive control - that influence the priority of domain specific information processing (Fan et al., 2009). These attentional networks are responsible for producing and maintaining a state of readiness in order to process non-specific impending inputs (alerting function), selecting the most relevant information from various inputs within and across modalities (orienting function), and detecting and resolving conflict among competing mental processes (executive control function) to make rapid and accurate responses (Petersen & Posner, 2012; Posner & Petersen, 1990). The Attention Network Test (ANT) (Fan, McCandliss, Sommer, Raz, & Posner, 2002) measures the efficiency of these three attentional functions and provides useful insights about attentional abilities of normal controls (Callejas, Lupianez, Funes, & Tudela, 2005; Fuentes & Campoy, 2008; Ishigami & Klein, 2010, 2011; Mackie et al., 2013; Martella et al., 2012), children (Abundis-Gutiérrez, Checa, Castellanos, & Rueda, 2014; Federico, Marotta, Adriani, Maccari, & Casagrande, 2013; Pozuelos, Paz-Alonso, Castillo, Fuentes, & Rueda, 2014; Rueda et al., 2004; Yaakoby-Rotem & Geva, 2014), and a variety of clinical populations (Fan et al., 2012; Marotta et al., 2015; Martella et al., 2014; Nestor et al., 2007; Neuhaus et al., 2010; Posner et al., 2002; Spagna et al., 2015).

In the past ten years, several papers have used a modified version of the ANT (the (lateralized ANT, LANT) to study the hemispheric lateralization of the attentional functions by presenting the stimuli in the LVF or in the RVF (Asanowicz, Marzecova, Jaskowski, & Wolski, 2012; Greene et al., 2008; Konrad et al., 2005; Marzecova, Asanowicz, KrivÁ, & Wodniecka, 2012; Poynter, Ingram, & Minor, 2010; Tao, Marzecová, Taft, Asanowicz, & Wodniecka, 2011). However, results have been controversial, mostly due to differences between the specific methodological parameters used in these studies. For example, hemispheric asymmetries in the three attentional functions were found when the distance between stimuli and the fixation point was greater than 5° of visual angle and in presence of invalid cue trials (the experimental conditions testing the reorienting function of attention) (Asanowicz et al., 2012), but not at smaller retinal eccentricities (Greene et al., 2008; Poynter et al., 2010). Overall, subtle interactions between each attentional function and the visual fields exist, and designing a lateralized version of the ANT that magnifies these interactions could benefit our understanding of these phenomena.

Another relevant aspect that needs further investigations is whether the RH also modulates the interaction among alerting, orienting and executive functions. Nowadays, there is evidence showing that pseudoneglect is often associated with reduced arousal (Bellgrove, Dockree, Aimola, & Robertson, 2004; Benwell, Thut, Grant, & Harvey, 2014; Manly, Dobler, Dodds, & George, 2005) suggesting that the alerting and orienting functions of attention interact. Behavioral interactions between these two attentional functions were first shown found by Callejas, Lupianez, and Tudela (2004) using a modified version of the ANT (Attention Network Task for Interactions; ANT-I) created to manipulate the alerting and the orienting components independently. By including an acoustic warning tone and a non-predictive visual cue in the paradigm, the ANT-I successfully showed the interaction between the three attentional functions in adults (Callejas et al., 2004, 2005; Federico et al., 2013; Fuentes & Campoy, 2008; Ishigami & Klein, 2011; Martella, Casagrande, & Lupianez, 2011; Martella et al., 2012; Poynter et al., 2010; Roca, Castro, Lopez-Ramon, & Lupianez, 2011), as well as in clinical populations (Casagrande et al., 2012; Fuentes et al., 2010; Marotta et al., 2015; Martella

et al., 2014). Interestingly, by using a lateralized version of the ANT-I with neglect patients, Chica et al. (2012) found that the presentation of the acoustic warning reduced the orienting deficit to left-sided target as well as the interference of flankers in the neglected visual field, thus facilitating conflict resolution. This study showed that conflict resolution could be improved in RH damaged patients by increasing the level of alertness and by modulating the orienting function, and opened to the possibility of creating behavioral interventions targeted on the attentional deficits of specific clinical populations.

The two hemispheres are specialized in the processing of distinct information, a phenomenon called functional cerebral asymmetries (FCA) (Corballis, 2009; Hugdahl, 2005; Ocklenburg et al., 2012), however, it is still unknown whether different types of imperative stimuli modulate the RH advantage for the attentional functions. Specifically, there is evidence showing that while the efficiency of the RH is greater for the processing of spatial information, the LH is specialized for the processing of verbal/semantic information, and that such asymmetries have an impact on the executive control function (see Ocklenburg et al., 2012 for a review). Further, the difficulty of the task to be performed interacts with the possibility to show hemispheric asymmetries in experimental paradigms. However, some authors propose that increasing task complexity would result in a reduction of hemispheric asymmetries due to the recruitment of areas in both hemispheres to resolve the task (Weissman & Banich, 2000; Welcome & Chiarello, 2008), while other authors have proposed that the functional asymmetries can be detected only in high perceptual load conditions, when greater attentional control is needed to solve the task, (Asanowicz et al., 2012; Evert et al., 2003). Thus, the role of key factors modulating the interactions between the three attentional networks and the two hemispheres is yet to be clarified.

The present study investigated the hemispheric effects on the attentional functions under different conflict conditions. In a recent study (Spagna et al., 2014), we examined the efficiency and interactions among the attentional functions under different conflict conditions by testing the impact of different type of imperative stimuli on conflict processing, and showed that the use of directional stimuli (i.e., arrows) modulates the executive control function to a greater extent than when non-directional stimuli are used (e.g., colored fruits). Further, the directional value of this set of stimuli modulated the orienting effect (i.e., a greater orienting effect was found when arrows were used as flankers and targets than with other sets of stimuli) due to the directional value of this specific stimuli, which resulted in an interaction between the executive control and the orienting functions of attention. Based upon those results, we explored the efficiency and interaction of the attentional functions in the visual fields when different types of imperative stimuli are used. We employed two different versions of the LANTI, in which arrows (LANTI-A) or fruits (LANTI-F) are used as imperative stimuli. For the LANTI-A, we predicted similar results than those found in Chica et al. (2012) for the healthy control group (i.e., a greater orienting effect for left-sided target indicating a RH advantage for this function). The LANTI-F was created to maximize the interactions between the three attentional functions and highlight the synergy between the three attentional functions needed to efficiently interact with complex environments. In the LANTI-F, the orienting function is manipulated independently from both alerting and the flanker conflict. We expect to replicate the greater orienting effect for left-sided targets found in the LANTI-A, and to magnify subtle interactions between the attentional functions and the visual fields that previous studies have failed to detect, such as the reduction of the conflict effect for left-sided target when an alerting tone and a valid cue are presented.

2. Materials and method

2.1. Participants

Forty-eight students (38 female; mean age = 25 ± 2.57) signed an informed consent before participating as volunteers in the study. The local ethical committee of Sapienza, University of Rome approved the study. All participants were right-handed, with a hand preference equal or greater than 85%, as assessed by the Italian version of the Edinburgh Inventory Questionnaire (Salmaso & Longoni, 1985), had normal or corrected-to-normal vision, and were unaware of the purpose of the study. The experiments were performed in accordance with the ethical standards of the Declaration of Helsinki.

2.2. Apparatus

Visual stimuli were presented on a 17 CTR monitor with a screen resolution of 1024×768 pixels, while the auditory warning was presented through headphones (Trust, Quasar Headset). A PC running E-Prime software controlled the presentation of the stimuli, timing operations, and data collection. Responses were gathered through a standard mouse (Trust, USB Optical Mouse MI-2275F). A chin rest was used to prevent head movements.

2.3. Lateralized ANTI-Arrows (LANTI-A)

2.3.1. Stimuli

Each trial began with the presentation of a central cross of 1° (degrees of visual angle). The stimuli consisted of a row of five black arrows, presented on a grey background. The target was an up- or down-pointing arrow flanked on each side by two arrows indicating either the same direction (congruent trials) or the opposite direction (incongruent trials). A single arrow consisted of 0.58° of visual field and the contours of adjacent arrows or lines were separated by 0.06° of visual field. The stimuli (one central arrow plus four flankers) subtended a total of 3.27° of visual field. The target and flankers were presented in the left or in the right visual field, 5° from the fixation point. The cue, in the form of an asterisk of 1° , could be valid, indicating the exact position where the target would appear, or invalid, indicating the position opposite to where the target would appear. For the no cue condition, no stimulus was presented. The auditory warning stimulus was 2000 Hz and lasted 50 ms.

2.3.2. Procedure

Participants were tested individually in a silent and dimly illuminated room, at a 57 cm distance from the computer screen. Each trial began with a fixation period of variable duration (400–1600 ms). This was followed by a warning stimulus lasting 50 ms in 50% of the trials. After a fixed inter-stimulus interval (ISI) of 350 ms, a cue of 50 ms was presented. In the valid condition (33% of the trials) an asterisk appeared in the same position of the target; in the invalid condition (33%) the target appeared in the opposite position than the one signaled by the cue; in the no-cue condition no orienting stimulus was presented. After a stimulus onset asynchrony (SOA) of 400 ms, target and flankers were presented for 150 ms and participants had a limit of 3000 ms to respond. The fixation point was at the center of the screen throughout the trial. The sequence of the events for each trial is shown in Fig. 1.

Participants performed one practice block of 24 trials, followed by three experimental blocks of 72 trials each. Overall participants completed 18 valid trials, 18 invalid trials, and 18 no-cue trials for each flanker and warning condition. Trials were randomly

presented within each block. Each task comprised 216 trials, for a total duration around 40 min. Participants were instructed to fixate the central cross and to respond as quickly and accurate to the target. The task was to identify the direction of the peripherally presented arrow by clicking the right or left button on the mouse according to the direction indicated by the target.

2.4. Lateralized ANTI-Fruits (LANTI-F)

The procedure was the same as in the LANTI-A, with the exception of the imperative stimuli used. In the LANTI-F target and flanker stimuli were red strawberries and yellow pears. The stimuli were positioned with the four flankers that overlapped the border of an imaginary semicircle in which the target was at the center (Spagna et al., 2014). Participants were instructed to fixate the central cross, to discriminate the central fruit and to respond as quickly and accurately as possible, by clicking the right or left button on the mouse.

2.5. General procedure

In each experiment, half of the participants responded by pressing the right button of the mouse when the up-pointing arrow or the strawberry appeared on the screen and by clicking the left button when the down-pointing arrow or the pear were presented; for the other half, response buttons were inverted. The administration of the two experiments was counterbalanced among participants. Procedure and stimuli are shown in the Figs. 1 and 2, respectively.

2.6. Data analysis

RT above or below 2 standard deviations (4.31%) were considered as outliers and then disregarded from analyses (Spagna et al., 2014). To investigate whether our tasks replicated results found in previous studies using the general ANTI structure, and to identify interactions also involving the visual field, a *Task* (LANTI-A, LANTI-F) \times *Visual Field* (left, right) \times *Warning* (absent, present) \times *Cue* (invalid cue, no cue, valid cue) \times *Flanker* (congruent, incongruent) repeated measures analysis of variance (ANOVA) was performed on RT of the correct responses. Also, according with results from a previous study (Asanowicz et al., 2012), ANOVAs with Visual Field as the independent variable and each attentional effect as the dependent variable, were separately made for each LANTI version. The effects of each of the three attentional functions, as well as their interactions, were operationally defined as a comparison of the reaction time between an experimental condition and a reference condition. The alerting effect was computed by comparing RT of trials in which an alerting cue preceded the presentation of the target (therefore, informing about the temporal onset) with RT of trials in which no alerting stimulus was presented. The orienting effect was computed by comparing RT of trials in which a valid spatial cue was presented with RT for trials in which an invalid cue was presented. Thus, a higher score can be interpreted as higher efficiency of orienting (Callejas et al., 2004; Posner, 1980). However, following the neuroanatomical model proposed by Corbetta, Patel, and Shulman (2008), orienting of attention is considered to be controlled by the two functionally separated systems: bilateral dorsal frontoparietal network controls both voluntary and automatic orienting, while the right-lateralized ventral frontoparietal network subserves reorienting to relevant stimuli. Therefore, a full range of data is needed to interpret the potential VF asymmetries of the orienting index. For instance, the LVF advantage in the invalid cue condition would indicate RH superiority in reorienting to uncued targets, which is controlled by the ventrolateral network (De Schotten et al., 2011; Foxe et al., 2003; Shulman et al., 2010). To this end, additional analyses

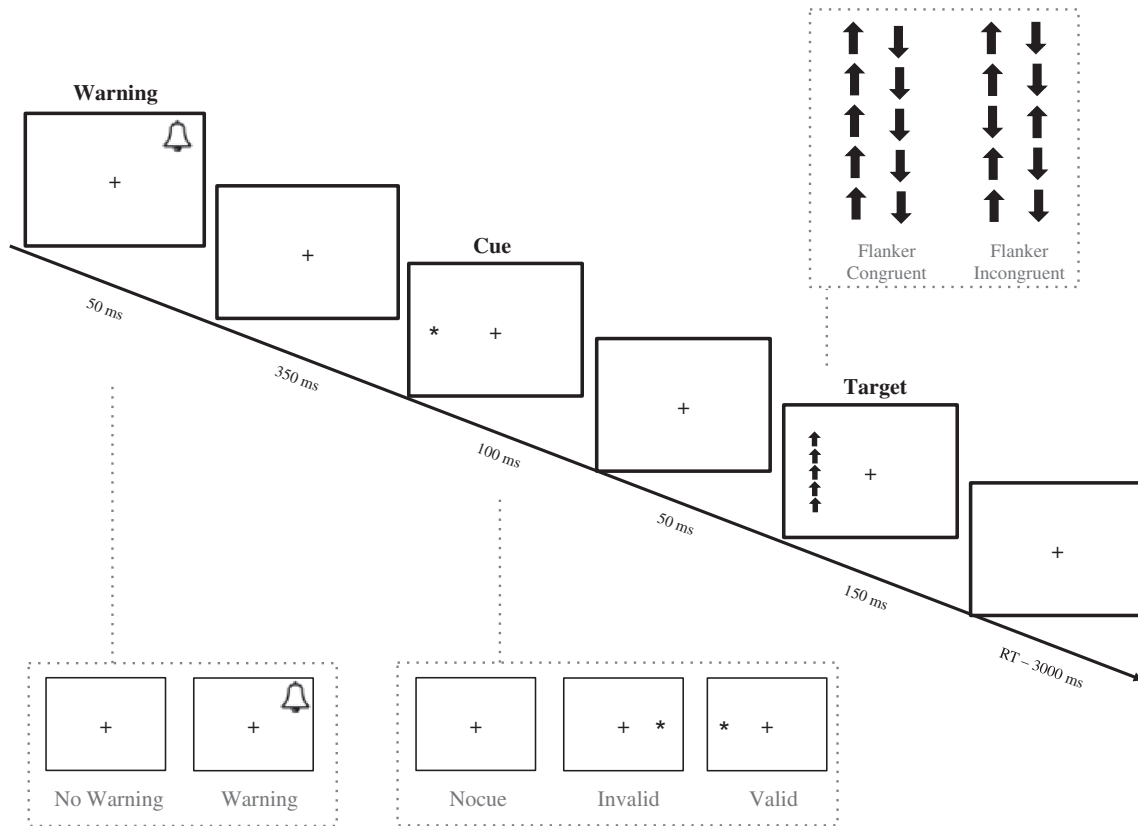


Fig. 1. Schematic of a trial in the LANTI. In this task, a warning stimulus, in the form of 50 ms 2000 Hz tone, and a cue, represented by an asterisk appearing for 100 ms in the left/right visual field, preceded the presentation of the target (a left- or right-pointing arrow). Participants must indicate the direction of the central arrow, while ignoring the flanking stimuli, by pressing the appropriate button on the mouse.

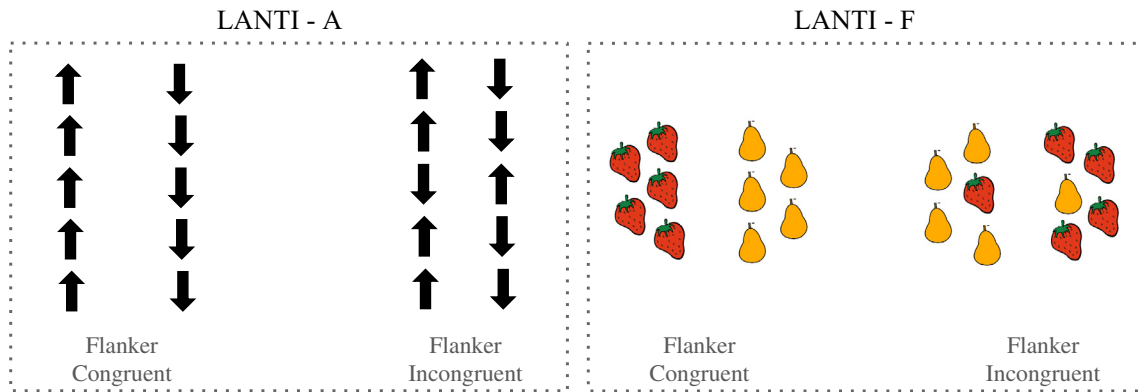


Fig. 2. Imperative stimuli used in the LANTI-A (left panel) and LANTI-F (right panel).

of variance were conducted (see attentional effects paragraph). Finally, the index of executive network was assessed by comparing reaction times for targets flanked by congruent distracters with those flanked by incongruent distracters (i.e. conflict effect). To further analyze the interactions planned comparison were used. In order to counteract the problem of multiple comparisons, Bonferroni correction was applied to the analyses.

3. Results

Table 1 shows the mean RT (\pm SD) for each experimental condition for the two tasks, while Table 2 shows the three attentional effects (in ms) separately for each visual field and task. The overall

accuracy for the LANTI-A was 95.80% (\pm 5.36%) and for the LANTI-F was 97.07% (\pm 2.79%). Data from one subject were excluded due to altered output from the software. Effects and interactions not listed below were not significant.

3.1. Lateralized attentional network test for interaction

The main effects of *Task* ($F_{(1,46)} = 29.11$; $p < 0.0001$; $\eta_p^2 = 0.39$), *Warning* ($F_{(1,46)} = 51.32$; $p < 0.0001$; $\eta_p^2 = 0.53$), *Cue* ($F_{(1,46)} = 58.23$; $p < 0.0001$; $\eta_p^2 = 0.56$), and *Flanker* ($F_{(1,46)} = 298.34$; $p < 0.0001$; $\eta_p^2 = 0.87$) were significant. Participants were faster in the LANTI-F than in the LANTI-A task (622 ms vs. 704 ms), they were faster when the warning was present compared to when it was absent

Table 1
Mean reaction time in ms (±SD) for each condition of the LANTI-A (upper panel) and LANTI-F (lower panel).

	Left visual field						Right visual field					
	No warning			Warning			No warning			Warning		
	Invalid	No cue	Valid	Invalid	No cue	Valid	Invalid	No cue	Valid	Invalid	No cue	Valid
<i>LANTI-A</i>												
Congruent	699 (128)	715 (147)	654 (173)	668 (123)	657 (131)	625 (157)	699 (151)	701 (125)	658 (140)	665 (135)	673 (166)	609 (142)
Incongruent	765 (140)	749 (128)	154 (199)	776 (140)	715 (118)	675 (139)	775 (145)	764 (147)	723 (142)	774 (128)	733 (172)	697 (151)
<i>LANTI-F</i>												
Congruent	628 (158)	621 (124)	581 (126)	572 (108)	599 (186)	567 (136)	633 (159)	641 (182)	590 (129)	603 (124)	576 (157)	555 (121)
Incong-ruent	660 (129)	674 (132)	646 (147)	654 (139)	609 (104)	622 (124)	682 (160)	680 (139)	633 (119)	657 (159)	624 (113)	611 (115)

Table 2
The three attentional effects (in ms) in the left and right visual fields, separately for the each tasks.

	LANTI-A				LANTI-F			
	Mean LVF	Mean RVF	F _(1,46)	p =	Mean LVF	Mean RVF	F _(1,46)	p =
Alerting	24	28	<1	0.74	25	28	<1	0.72
Orienting	58	56	<1	0.91	24	46	4.26	0.04
Conflict	73	84	1.44	0.23	59	51	<1	0.43

(646 ms vs. 679 ms), when the cue was valid (636 ms) compared to when it was invalid (682 ms; $p < 0.001$) and when no cue was presented (671 ms; $p < 0.001$); further, they were faster in the nocue condition compared to the invalid cue condition ($p < 0.05$), and in the congruent (648 ms) compared to the incongruent condition (702 ms). The interaction between *Task* and *Cue* was significant ($F_{(2,92)} = 3.38$; $p < 0.05$; $\eta_p^2 = 0.07$). Planned comparisons indicated that the difference in RT between the invalid and the valid condition was greater in the LANTI-A (728 vs. 671 ms; $F_{(1,46)} = 64.62$; $p < 0.001$) compared to the LANTI-F (636 vs. 601 ms; $F_{(1,46)} = 47.22$; $p < 0.001$). The interaction between *Warning* and *Cue* ($F_{(2,92)} = 4.21$; $p < 0.05$; $\eta_p^2 = 0.08$) indicated that the difference in RT between invalid and valid trials was greater in the warning condition (693 vs. 651 ms; $F_{(1,46)} = 40.84$; $p < 0.001$) compared to

the no warning condition (671 vs. 620 ms; $F_{(1,46)} = 760.03$; $p < 0.001$). The interaction between *Task* and *Flanker* was significant ($F_{(2,92)} = 11.69$; $p < 0.001$; $\eta_p^2 = 0.21$) and indicated a greater RT difference between incongruent and congruent trials in the LANTI-A (739 vs. 669 ms; $F_{(1,46)} = 189.04$; $p < 0.001$) compared to the LANTI-F (646 vs. 597 ms; $F_{(1,46)} = 136.24$; $p < 0.001$). The *Cue* × *Flanker* interaction was significant ($F_{(2,92)} = 7.14$; $p < 0.01$; $\eta_p^2 = 0.13$). Planned comparisons indicated that the difference in the RT between incongruent and congruent trials was greater in the invalid trials (718 vs. 646 ms; $F_{(1,46)} = 194.12$; $p < 0.001$) compared to both nocue (693 vs. 648 ms; $F_{(1,46)} = 60.24$; $p < 0.001$) and valid (666 vs. 605 ms; $F_{(1,46)} = 143.37$; $p < 0.001$) conditions. The *Warning* × *Cue* × *Flanker* interaction was significant ($F_{(2,92)} = 3.56$; $p < 0.05$; $\eta_p^2 = 0.07$) and the five-factor interaction was marginally significant ($F_{(2,92)} = 2.90$; $p = 0.06$; $\eta_p^2 = 0.06$). To further analyze this interaction, an ANOVA *Task* (LANTI-A, LANTI-F) × *Warning* (Absent, Present) × *Cue* (Invalid, Valid) × *Flanker* (Congruent, Incongruent) was conducted by considering the difference between RT in the left and right visual fields (RVF - LVF) as the dependent variable.

3.2. Laterality difference of the attentional effects and interactions

To further analyze the marginally significant five-factor interaction, an ANOVA *Task* (LANTI-A, LANTI-F) × *Warning* (Absent,

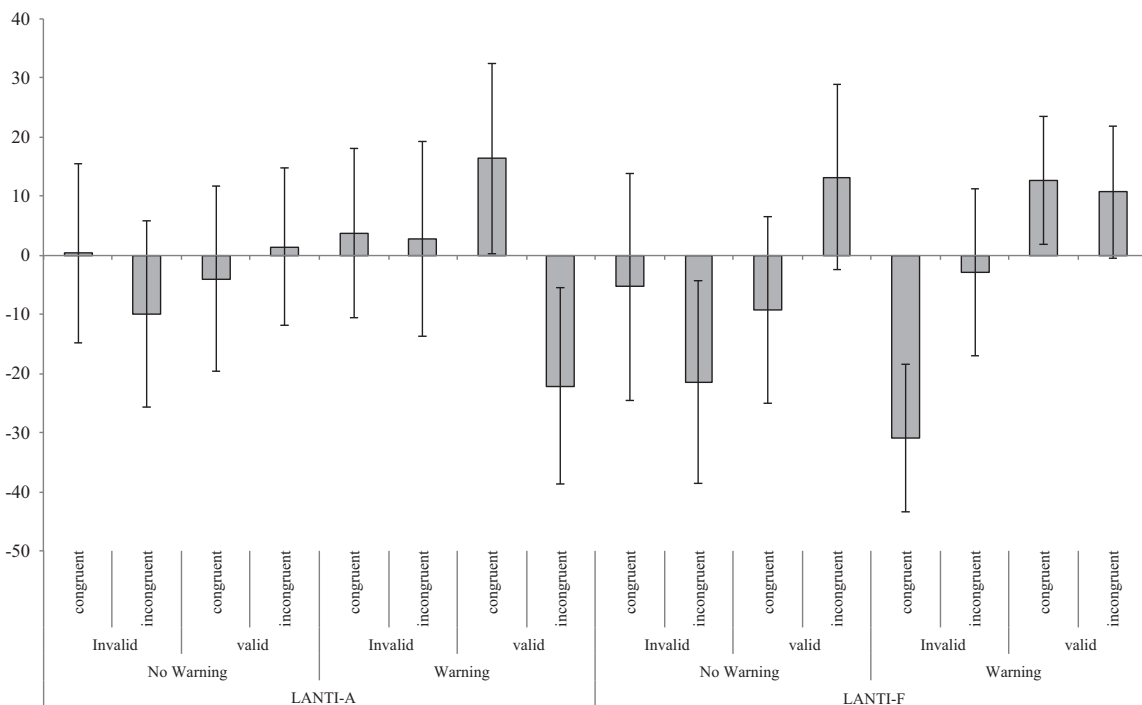


Fig. 3. Group performance in each condition as a function the Laterality Index (LVF - RVF) in both the LANTI-A (left panel) and LANTI-F (right panel).

Present) \times Cue (Invalid, Valid) \times Flanker (Congruent, Incongruent) was conducted by considering the difference between RT in the left and right visual fields (RVF - LVF) as the dependent variable. The ANOVA on the laterality index showed that the *Warning \times Cue \times Flanker* interaction was significant ($F_{(1,46)} = 6.46$; $p < 0.05$; $\eta_p^2 = 0.13$). All the other effects and interactions were not significant ($p \geq 0.14$). To further analyze this three-way interaction a *Warning \times Cue \times Flanker* ANOVA was separately performed for the LANTI-A and LANTI-F (see Fig. 3). For the LANTI-A, none of the effects and interactions was significant ($p \geq 0.10$). For the LANTI-F, the main effect of cue was significant ($F_{(1,46)} = 4.26$; $p < 0.05$; $\eta_p^2 = 0.09$), showing a higher laterality index in the invalid compared to the valid condition (-15 ms vs. 7 ms). Further, the *Warning \times Cue \times Flanker* interaction was significant ($F_{(1,46)} = 4.63$; $p < 0.05$; $\eta_p^2 = 0.09$), and revealed that the difference between invalid and valid conditions was statistically different only when the warning was present and the trials were congruent (-31 ms vs. 13 ms; $F_{(1,46)} = 70.02$; $p < 0.05$). This difference was not significant for warning present and incongruent trials (-3 ms vs. 11 ; $F < 1$), warning absent and incongruent trials (-22 ms vs. 13 ; $F_{(1,46)} = 2.22$; $p = 0.14$), and warning absent and congruent trials (-5 ms vs. 9 ms; $F < 1$). However, none of the post hoc tests reached significance after using Bonferroni correction for multiple comparisons.

3.3. Attentional effects

To further examine the hemispheric lateralization of attentional effects, one-way ANOVAs with the *Visual Field* (Left, Right) as a factor were separately performed for each *Task* (LANTI-A and LANTI-F) on each attentional effect (see Fig. 4).

Alerting effect. For both tasks the visual field was not significant ($F < 1$).

Orienting effect. The orienting effect was significant for the LANTI-F ($F_{(1,46)} = 4.26$; $p < 0.05$; $\eta_p^2 = 0.09$), but not for the LANTI-A ($F < 1$). Importantly, in the LANTI-F, the RVF–LVF

difference yielded only 7 ms in the valid cue condition, whereas in the invalid cue condition, the LFV advantage reached 15 ms. Thus, the reorienting to invalidly cued targets was more efficient for the targets presented in the LVF. These results are in line with the data of Asanowicz et al. (2012), who reported VF asymmetry only for the invalid cue condition.

Conflict effect. The difference in the conflict effect between the two visual fields was not significant in both the LANTI-A ($F < 1.44$; $p > 0.23$) and LANTI-F ($F < 1$).

4. Discussion

In this study, we examined the differential contribution of the two hemispheres to the attentional functions by testing the efficiency and interaction of the alerting, orienting, and executive control of attention in the LVF and RVF under different conflict conditions. To achieve this aim, participants were tested with two lateralized variants (LANTI-A and LANTI-F) of the Attention Network Test for Interaction (Spagna et al., 2014).

Overall, both versions of the ANTI allowed for clear identification of the three attentional functions and their interactions. Indeed, the principal findings from Callejas et al. (2004) were replicated: significant main effects for the Warning Signal, the Visual Cue and the Flanker conditions, as well as main expected interactions were observed. Moreover, results confirmed the differential impact produced by different imperative stimuli on the orienting and executive control functions found in our previous study (Spagna et al., 2014): orienting and conflict effects were greater in the LANTI-A than in the LANTI-F. Also, the results of the present study showed that the enhancement produced by a warning tone on the orienting function consistently found in previous studies using the ANTI (Asanowicz et al., 2012) was higher in the LANTI-A than in the LANTI-F. This result may be explained by the modulation produced by the use of directional imperative stimuli on the orienting functions (ANTI-A) (Corbetta et al., 2008; Shulman et al., 2010).

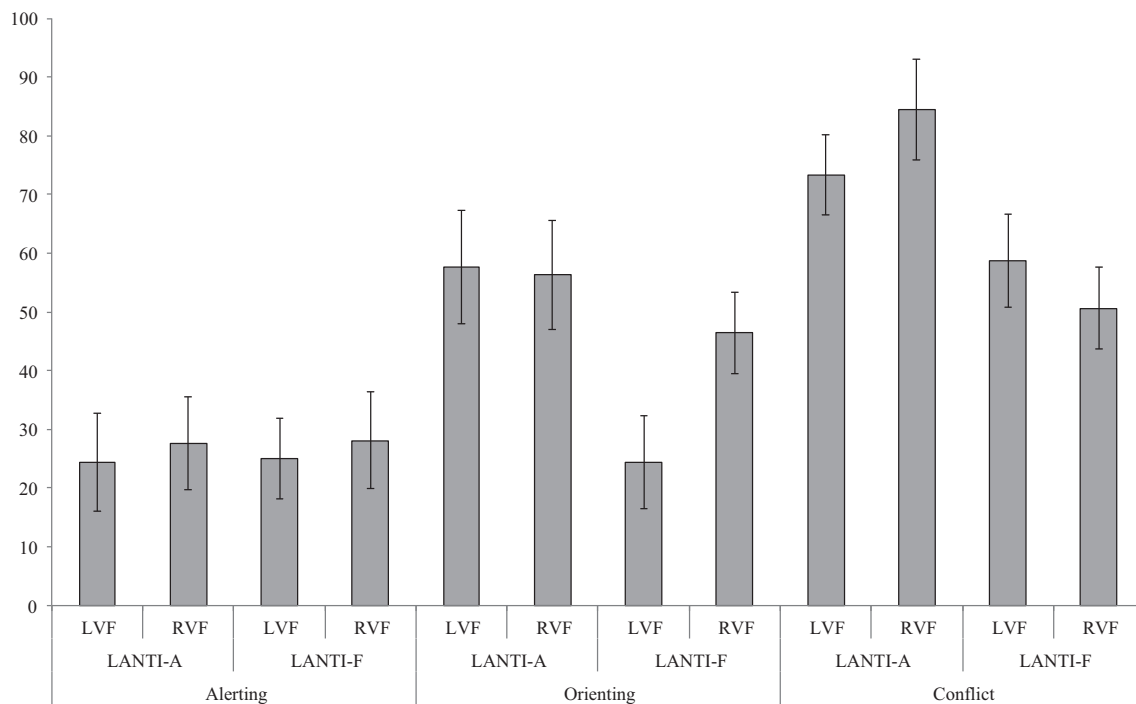


Fig. 4. The alerting (left), orienting (middle), and conflict (right) effects as a function of the visual field and task.

Hemispheric asymmetries were observed for the orienting function of attention. Specifically, a LVF advantage was found in the invalid orienting cue condition, while no VF asymmetry for the selection of the targets in the valid cue condition was observed, in the LANTI-F. These results are consistent with previous behavioral findings (Asanowicz et al., 2012; Chica et al., 2012; Evert & Oscar-Berman, 2001; Evert et al., 2003) and fit with neuroanatomical model of attention proposed by Corbetta et al. (2008). According to this model, bilateral dorsal frontoparietal network controls both voluntary and automatic orienting, while the right-lateralized ventral frontoparietal network subserves reorienting to unexpected but behaviorally relevant stimuli that appear outside the current focus of attention. Therefore, this model seems to predict a LVF advantage in the invalid cue condition and no asymmetry in the valid cue condition, which is in accordance with our results, thus suggesting greater efficiency of the RH in reorienting of attention. However, these results were only found when non-directional stimuli were used as imperative stimuli. A possible explanation for the lack of hemispheric asymmetries in the task with directional stimuli comes from the hypothesis stating that greater inter-hemispheric activity follows the increase of task complexity (Weissman & Banich, 2000; Welcome & Chiarello, 2008). According to this hypothesis, in order to perform the more complex (as shown by the significantly greater mean RT and conflict effect in the LANTI-A compared to the LANTI-F) may have recruited cortical areas needed for the conflict resolution located in both hemispheres. Alternatively, the greater conflict effect produced by directional imperative stimuli, compared to the stimuli used in the LANTI-F, may have challenged our participants more towards the conflict resolution and, in turns, may have hidden (in terms of statistical observed power) or affected the interactions between the attentional networks and the visual fields (see also Magen & Cohen, 2007, 2010). It should also be noted that the only previous study (Asanowicz et al., 2012) that found an interaction between the orienting function and the visual fields when directional stimuli were used had a much larger sample size than the our study, which may indicate the need of greater statistical power to identify such subtle yet significant interaction in complex tasks.

Participants were marginally best able to reorient their attention (due to the presentation of an invalid cue) when the stimuli were presented in the LVF than in the RVF when they were also alerted by a warning signal and when the discrimination of the target was easier (i.e., congruent flankers) (LVF = 572 ms vs. RVF = 603 ms). We therefore speculate that subtle (but only marginally significant) interactions between the three attentional networks and the visual fields exist, and that the level of alertness and the attentional load modulates the hemispheric asymmetry for the reorienting process. In fact a RH advantage emerges only when the task is easier (LANTI-F) and the executive system is less challenged (congruent condition). Apparently this finding is in contrast with previous studies suggesting that functional asymmetries become apparent only under high attentional demands (Evert et al., 2003). However, Evert and colleagues used a spatial cueing task with a low or high perceptual load while in our study we make use of a more complex task (ANTI), which allow evaluating not only the orienting, but also the alerting and the executive functions independently. Furthermore, in the study of Evert et al. (2003) the attentional demand of the task was manipulated by changing the perceptual load, while in our study we varied the attentional demand by manipulating the involvement of the executive system (i.e., ANTI-A vs ANTI-F and congruent vs incongruent condition). In our opinion, using our set of non-directional stimuli as target and flankers may better serve the goal of examining the interactions among the attentional networks, by avoiding the modulation produced by imperative stimuli conveying directional information on both the orienting and executive functions.

In conclusion, a LVF advantage was found when a target occurred in an unattended location (e.g. invalid trials), only with the LANTI-F, but not with the LANTI-A, suggesting at least in the former task the RH dominance in the control of the reorienting of attention. As a whole, results suggest that the advantage of the RH in the reorienting process is mainly present when the task requires a smaller attentional load. Our study adds more evidence to the hemispheric asymmetry of the orienting of attention, and informs about patterns of interactions between the attentional networks and the visual fields across different conflicting conditions. This field of research will benefit from the use of the LANTI versions proposed together with neurophysiological measures to further identify the neural basis associated with the visual field asymmetries of the three attentional networks.

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