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Research report

Salience-based progression of visual attention

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ABSTRACT

Cognitive and computational models assume that visual attention is directed to the most salient stimulus in a given scene, and physiological models suggest the attribution of salience might depend on the extrageniculate pathway, involving the superior colliculus and pulvinar. Empirical findings support these models. Another assumption is that attention progresses from the most to the least salient item until a target is found. We have therefore attempted to investigate whether behavioral nasal–temporal hemifield asymmetries in healthy humans are present in the salience-based progression of attention. Hemispheric asymmetries have also been investigated. Healthy volunteers were presented with brief lateralized displays containing three stimuli of unequal sizes (one target and two distractors) and asked to make a judgment regarding the target. In each new trial, each of the three stimuli was chosen randomly with equal probability of being the target. The expected salience-based progression was found in both response times and accuracy. While no temporal-nasal asymmetries were found in accuracy for displays processed by the left hemisphere, a well-marked asymmetry was found for displays processed by the right hemisphere. The progression slope was quite steep for nasal displays and nil for temporal displays. A companion experiment replicated the results, another one ruled out any sensory interpretation of the results, and a last one ruled out the possibility that the results were due to saccadic eye movements. What distinguishes the two pathways is therefore not whether or not they generate salience, but the strength of the activity that differentiates the visual input. Furthermore, the involvement of the right extrageniculate pathway in the fineness of the perceptual analysis that follows orienting of attention seems to take place independently of the salience of the attended item.

1. Introduction

Visual salience[1] is not a physical property of an item, but the relationship between that item and other items in the scene. It results from a comparison of elementary visual features and serves to order inputs for further processing. This ordering, or hierarchy, is thus the aspect likely to be the most relevant for orienting attention. According to attention models specific qualities of visual input, like color, size, form and luminance, are represented in specialized feature maps [1] that compute the differences between each item and its neighbors within a particular feature dimension. These differences feed into a salience map that sums them up in such a way that the relative distinctiveness of each item is represented at its location in a featureless manner [2–4]. Attention is then directed to the location with the greatest activity and will progress in a salience-based fashion until a target is found. Thus, multiple underlying computations contribute to the emergence of two distinct – but related – salience-based phenomena: (a) attention capture by the most salient item in the scene and (b) attention progress from the most salient item to the least salient item.

Empirical demonstrations of attention-capturing properties of salient items have frequently been provided over the past decades [4,5], and there is no doubt this phenomenon exists. Indirect evidence that different levels of salience have different effects on performance, which may be considered similar to the salience-based progression of attention [2,4,6], is provided by multiple-cue paradigms. For instance, Kean and Lambert [7] investigated the effects on orienting of attention of two brief and simultaneous peripheral pre-cues that preceded a target at various time intervals. The two pre-cues differed in their degree of luminance insofar as one was brighter than the other. In one condition, where the target was just as likely to appear near the bright cue as the dim cue, saccadic latencies were faster when it appeared near the bright cue, and this effect was observed even at very short cue-to-target

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[1] There is general confusion between visual salience, depending on input, and internal salience, which depends on task sets. Here, the term salience is used only to denote the former, with "relevance" being reserved for the latter with respect to recent cognitive [6] and neurophysiological [13] models.

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intervals (<50 ms). Yet, there seems to be some confusion between luminance of a single item (i.e., its physical strength) and salience (i.e., its difference in relation to its neighbor) since there was no evidence that, when presented alone, each of the two cues could elicit effects similar to the other. Such a finding is essential for rejecting a luminance-based (i.e., sensory) account of the results in favor of a salience-based account, since visual processing speed depends on stimulus intensity [8]. Indeed, Wright and Richard [9] suggested that such effects are mediated not by attention but by sensory processes. Thus, a safe interpretation of the effects of multiple-cue paradigms would mean demonstrating that at least the two extreme levels of the manipulated stimulus dimension have similar effects when presented alone.

Bearing in mind that evidence points to several areas as underlying visual salience (the pulvinar [10]; the parietal cortex [11]; some areas of the occipito–temporal pathway [12]), Fecteau and Munoz [13] proposed that the candidate neural correlates require input to the intermediate layers of the superior colliculus (SC) from late stations in the visual hierarchy, rather than from areas involved in early visual processing [14,15]. However, drawing on physiological, psychophysical and computational evidence, Li ([16]; see also [2]) proposed that the visual area most likely to provide a salience map is V1. Interestingly, the occipito–temporal and lateral intraparietal areas mentioned by Fecteau and Munoz [13], which are key structures for the expression of attention in the triangular circuit theory [17], receive input from both the V1 area (originating in the lateral geniculate body; LGB; i.e., geniculate pathway) and the pulvinar (either indirect projections from the retina to the SC then the pulvinar, or direct retino–pulvinate projections; i.e., extrageniculate pathways). These arrangements suggest that, whether provided by the V1 area through the LGB, the SC or the pulvinar, salience could be built on combined input conveyed through both pathways. Stimulating each of these two pathways with the same signal should therefore provide evidence of how they contribute to salience and how salience is used thereafter as a basis for directing attention.

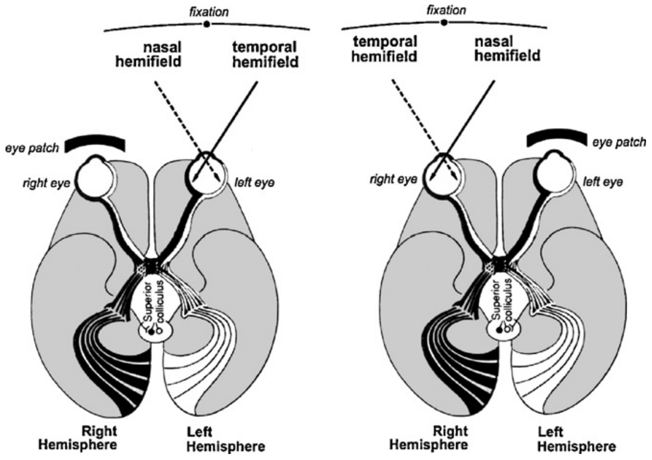

Fig. 1. Transfer of visual information under monocular viewing conditions. The left–right inversion is due to the fact that the brain is seen from below. Stimuli from the left hemifield of each eye (dotted arrow) are projected to the right hemisphere (pathway in white) and stimuli from the right hemifield of each eye (solid arrow) are projected to the left hemisphere (pathway in black). Stimuli from the temporal hemifield of each eye are transferred through crossed fibers to the contralateral hemisphere (left eye-to-right hemisphere; right eye-to-left hemisphere) and some of these fibers are directed towards the contralateral superior colliculus and pulvinar. Stimuli from the nasal hemifield of each eye are transferred through uncrossed fibers to the ipsilateral hemisphere (left eye-to-left hemisphere; right eye-to-right hemisphere) but their projections towards the superior colliculus and pulvinar are very limited.

Nasal–temporal field asymmetries (albeit equivocally) are taken as signs of differences in geniculate and extrageniculate processing [18]. Because the extrageniculate pathway is a phylogenetically older visual system, retinal projections to the superficial layers of each SC convey information mainly from the contralateral hemifield [19]. Under monocular viewing conditions, information from both the temporal (i.e., physically closest to the temple) and nasal (i.e., physically closest to the nose) hemifields projects to both the lateral geniculate body and the SC. Nasal–temporal numerical asymmetries are thus present in both pathways [20] but information from the temporal field is represented more in the SC than information from the nasal field [18]. The left hemifield of the left eye is represented more in the right SC, and the right hemifield of the right eye is represented more in the left SC. Thus, reversing the stimulated eye reverses whether the left or right hemifield is temporal or nasal, and whether the stimulated hemisphere is the left or right (Fig. 1). Correspondingly, Bompas et al. [21] found nasal–temporal asymmetries even for S cone stimuli, a type of color contrast invisible to the SC,[2] which suggests that the nasal–temporal asymmetries are not diagnostic of extrageniculate mediation. Neuroimaging techniques showed however that the temporal hemifield is indeed over-represented in the human contralateral SC [22], whereas such asymmetry is not found in the LGB and V1. Besides, selective unilateral lesions of the SC in humans [23] eradicate attentional effects of stimuli presented in the contralesional temporal field. The nasal–temporal asymmetry of the direct retino–pulvinate projections is less contradictory than that of the indirect retino–tecto–pulvinate pathway [20,24,25]. Neuronal tracing techniques have demonstrated that all three classes of retinal cells project directly to the retinotopically organized inferior portion of the pulvinar (Pi), with konio cells more numerous than magno, and parvo cells the least numerous [25]. It is noteworthy that in primates both the parvo and konio cells are color opponent [26–28]. Furthermore, the primate [24] and human [23] pulvinar exhibits a real numerical nasal–temporal asymmetry. Thus, direct retino–pulvinate projections of the extrageniculate pathway may explain the functional nasal–temporal asymmetries found in blindsight [18] and in experiments using S cone stimuli [21], and the residual detection of chromatic changes in both hemianopic monkeys and humans [29]. It may also explain why lesions of the pulvinar eradicate involuntary capture by color changes [30]. Here, we shall be referring to both retino–tectal and the direct retino–pulvinate as extrageniculate pathways. If the geniculate and extrageniculate pathways both contributed towards salience and helped the progression of visual attention, but in a different way, as suggested previously, then nasal–temporal asymmetries were to be expected. Most brain areas proposed as generating salience receive input from both these pathways. It is therefore quite plausible that all structures are involved in generating visual salience, but their relative contributions depend on the result of processing taking place in each pathway. Thus, instead of asking which brain structure generates visual salience, we asked what contribution signals conveyed through each of the two input pathways make to salience and the salience-based progression of attention.

To the best of our knowledge, no study has ever investigated the progression of attention in visual search or the role of the visual pathways in the salience-based progression of spatial attention. Therefore, we used a modified version of a visual search paradigm (which, for sake of convenience, we have called the multiple salience level visual search task). This paradigm involves

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[2] Even though it has been established that neurons in the superficial layers of the SC show no color opponency, it is still not known whether these particular stimuli really are invisible to the SC. The authors also acknowledge that these stimuli produce some saccade effects, which are often held to be stimulus-driven, suggesting that they may trigger collicular activity.

simultaneously presenting three items of slightly different sizes to produce a hierarchy of salience based on size. In each new trial, the target is chosen to be one of the three items with equal probability, a classic way of reducing the incentive to direct attention deliberately towards one item rather than another [31]. Subjects are asked to make a discrimination judgment about one of the items, defined as the target, while maintaining fixation. When the biggest item is the target, response times (RT) are expected to be faster and accuracy higher than when one of the other two items is the target. This is evidence of attentional capture. Furthermore, RT is expected to be slower when the target is the medium-sized item and slowest when it is the smallest item, evidence of a progression of attention from the most to the least salient item. Accuracy is also expected to follow this pattern. The items are displayed briefly in either the left or right hemifield, and subjects are required to make a discrimination judgment about one of them (defined as the target). In Experiment 1 the task is performed under monocular viewing conditions so as to investigate nasal–temporal asymmetries and, by means of some combinations, hemispheric asymmetries (Fig. 1; the left field of each eye projects to the right hemisphere, and the right field to the left hemisphere). In view of the aforementioned studies, effects of attentional capture and salience-based progression are expected after stimulation of both the nasal and the temporal hemifields. Such effects may be more pronounced after stimulation of the temporal hemifield – as temporal field superiority effects in attention were reported previously – in that the establishment of a better defined salience hierarchy would render each item more distinct from the others allowing, therefore, attention to move faster across their locations.

We also conducted a companion experiment (Experiment 2) to investigate the possible sensory effects of the stimuli. Here, only the biggest or smallest of the items used in Experiment 1 were displayed. Subjects were asked to make the same judgment as before, again while maintaining fixation. Subjects who took part in Experiments 1 and 2 were the same, so half of them started with Experiment 1 and the other half with Experiment 2 in order to balance any effects of learning and fatigue. Experiment 3 aimed at replicating the results of Experiment 1. Finally, the control Experiment 4 conducted under binocular viewing conditions on a small sample of subjects aimed at ruling out the possibility to interpret the results in terms of systematic eye movements towards the target during its brief exposure.

2. Experiment 1: salience-based progression

2.1. Materials and methods

2.1.1. Subjects

Forty healthy volunteers, 20 males and 20 females, took part for course credits. Their mean age was 21.9 ± 2.4 years; they were all right-handed according to the Edinburgh laterality inventory (mean laterality: 0.90 ± 0.11; [32]), all had normal or corrected-to-normal vision, and were not under any medication. They all gave their written consent for their participation.

2.1.2. Stimuli and apparatus

The stimuli were three white outlined (1 pixel) squares of different sizes. From a viewing distance of 41 cm, the large, medium and small squares subtended an angular space of $0.73^\circ \times 0.73^\circ$ (surface: $27.04\,\text{mm}^2$), $0.57^\circ \times 0.57^\circ$ (surface: $16.81\,\text{mm}^2$) and $0.49^\circ \times 0.49^\circ$ (surface: $12.25\,\text{mm}^2$), respectively, with a luminance of 1.93, 1.59 and $1.18\,\text{cd/m}^2$, respectively. Each square had a 3-pixel gap and was rotated 0°, 90°, 180° or 270° clockwise. The target orientation was 0° (up) or 180° (down), with one distractor oriented 90° (right) and the other 270° (left). The three squares were presented at 30°, 90° and 150° clockwise in relation to the vertical (i.e., to the right of fixation) or 30°, 90° and 150° anticlockwise in relation to the vertical (i.e., to the left of fixation), at a distance of 3.8°.[3] The distance between two neighboring squares was 3.8°. The fixation point was a small white dot ($1.94\,\text{cd/m}^2$). All the stimuli were presented on the black background ($0.53\,\text{cd/m}^2$) of a Dell Latitude computer with a PentiumII 200 MHz processor. The experiments took place in a dimly lit room (mean luminance $0.2\,\text{cd/m}^2$).

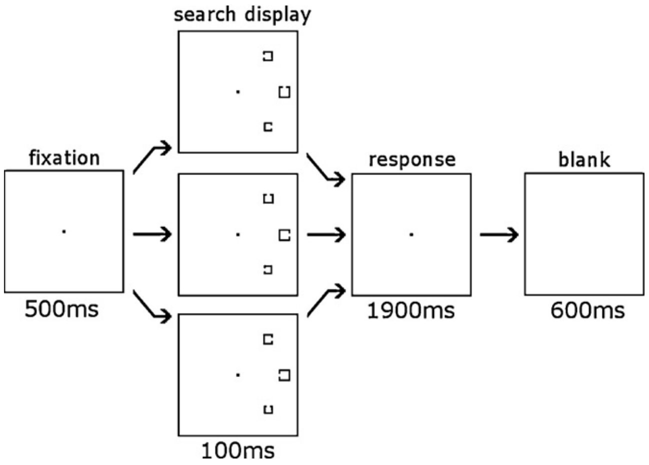

Fig. 2. Event from Experiment 1. Under monocular viewing conditions, subjects fixated a white dot presented on the center of a black computer monitor. The stimulus display was then presented for 100 ms either on the left or the right of fixation randomly. It contained three squares differing slightly in size and having a small gap on one of their sides, two of which had a gap on the left or right (distractors) and the third one on the top or bottom (target). The position and the size of the target varied randomly as to prevent subjects for developing incentives to attend preferentially the one or the other of the items. Subjects were asked to maintain fixation and to indicate as fast as possible whether the unique vertically gapped item had its gap on its top or the bottom.

2.1.3. Procedure

The procedure is depicted in Fig. 2. Each trial started with the presentation of a white fixation spot in the middle of the computer screen for 500 ms. The search display (i.e., the three squares) was then added for 100 ms to either the right or left of fixation (this short display duration was chosen to minimize saccades towards the items). One of the three squares was the target, and the other two were distractors. Each of them could be located randomly and equiprobably at one of three locations. The target was the big square in 33.3% of trials, the medium in 33.3% of trials, and the small in 33.3% of trials. In half of the trials, the target orientation was 0°. In the other half it was 180°. The location of the target (30°, 90° or 150° in relation to the vertical), its size (large, medium or small) and orientation (up or down) and the location of the search display (to left or right of fixation) occurred with equal probability and were randomly chosen by the computer in each new trial. Then, for a fixed period of 1900 ms the fixation spot remained on the screen, before being extinguished for 600 ms, which signaled the end of one trial and that the next was about to start. Subjects were encouraged to fixate the fixation spot throughout the experiment and, without trying to fixate the brief search display, to indicate the target orientation (up or down) as quickly and accurately as possible by pressing two pre-defined vertically-arranged response buttons with the major (up button) and index (down button) fingers of their

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[3] In primates, the 5 central degrees of the visual field are over-represented in the superficial layers of the SC [19]. Even though behavioral nasal–temporal asymmetries observed in humans were obtained with stimuli presented at larger eccentricities (8–10° [21,38,40], anatomical and physiological findings intimate that such effects should also be found in smaller eccentricities, even in central vision [63].

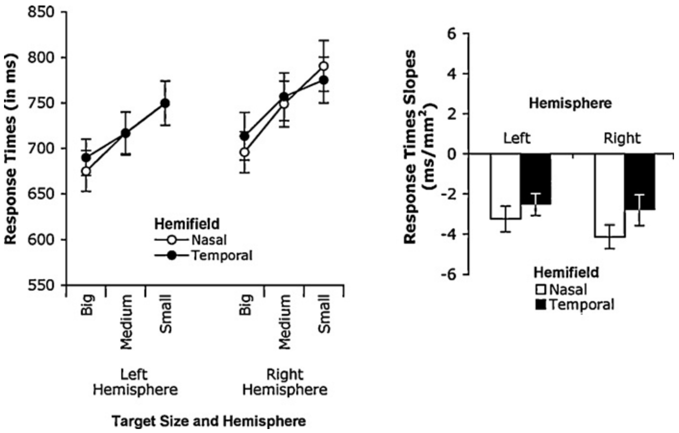

Fig. 3. (Left) Mean Response Times (±1SEM) in milliseconds observed in Experiment 1 plotted as a function of the target size, stimulated hemifield and the hemisphere to which the stimuli were projected. (Right) Mean Response Times Slopes (±1SEM) in milliseconds per additional square millimeter observed in Experiment 1 as a function of the stimulated hemifield and the hemisphere to which the stimuli were projected. The negative slopes indicate that each time the target would be 1 mm^2 bigger, Response Times would be faster. The more the slope is near 0, the faster is the deployment of attention.

right hand. All of the subjects were tested under monocular viewing conditions, such that half were tested with first their right eye open then the left, and *vice versa* for the other half, with a 5-min pause between. Monocular viewing was achieved with an eye-patch. Each subject completed a 30-trial training session, followed by an experimental 360-trial session (30 trials/search display location/target size/eye). RT and errors were recorded by the computer.

2.2. Results and discussion

2.2.1. Response times

Response times smaller than 100 ms and larger than 2000 ms were discarded as representing errors of anticipation and inattention, respectively. This exclusion accounted for less than 0.01% of the trials. We manipulated whether visual stimulation contralateral to a brain hemisphere was temporal or nasal. An analysis of variance (ANOVA) was therefore performed on the mean correct RT with the hemisphere (left *vs.* right), stimulated hemifield (nasal *vs.* temporal) and target size (big, medium, small) as within-subject factors. The main effect of hemisphere was significant ($F(1,39) = 12.62$; $p < 0.001$), with faster RT for the left hemisphere (LH; 716 ms) than the right hemisphere (RH; 747 ms). Processing of the small 3-pixel gap of each stimulus of the display requires fine-grain resolution, a mode of information processing characteristic of the LH [33]. It is not surprising therefore that displays projected to the LH were processed more quickly. The main effect of target size was significant ($F(2,78) = 37.8$; $p < 0.00001$). RT were faster when the target was the large square (694 ms), slower when it was the medium square (735 ms), and slowest of all when it was the small square (766 ms). This finding supports the salience-based hypothesis of orienting of attention [2,4,6]. No other main effects or interactions were found. The results are presented in Fig. 3(left panel).

2.2.2. Response time slopes

Since the overall performance as a function of the target size almost perfectly fit a linear function with respect to the surface of the target in mm^2 (mean determination coefficient $r^2 = 0.994$), progression slopes (α)[4] expressed in speed gain per additional square millimeter were analyzed as a way of investigating the progression of attention further. In general, and independently of the hemisphere and hemifield, the progression slope was -3.2 ms/mm^2. 95% of subjects exhibited such a negative slope ($p < 0.0001$ binomial), i.e. for each additional square millimeter subjects discriminated the target orientation ≈3 ms faster. This general slope was reliably different than 0 ($t(39) = 7.57$; $p < 0.000001$), as were the LH nasal, LH temporal, RH nasal and RH temporal slopes (all $ps < 0.0009$), meaning that RT progressed as a function of the target size. We then analyzed the progression of RT further by subjecting the corresponding slopes to an ANOVA with the hemisphere (left *vs.* right) and hemifield (nasal *vs.* temporal) as within-subject factors. A tendency towards significance was found only for the main effect of hemifield ($F(1,39) = 3.57$; $p < 0.067$), with progression slopes being slightly shallower for displays presented in the temporal hemifield (-2.7 ms/mm^2) than for those presented in the nasal hemifield (-3.7 ms/mm^2). Interestingly, overall shallower slopes for temporal displays were observed in 65% of subjects ($p < 0.04$ binomial), with the same asymmetric pattern found for both the left and right hemispheres. Thus, despite slopes being only marginally shallower in the temporal hemifield (Fig. 3, right panel), this is a quite regular finding across subjects. Similar results were obtained when progression slopes were computed as a function of the stimulus angular size (main effect of hemifield $F(1,39) = 3.57$; $p < 0.067$) or luminance (main effect of hemifield $F(1,39) = 3.35$; $p < 0.075$).

2.2.3. Response times distribution

We also analyzed the distribution of correct RT (10280 correct trials over a total number of 14,400 presented trials, i.e., 71.3%) as a way of investigating the locus of the changes observed in RT. Overall, when the target was the big item, there was a dominance of fast RT (300–700 ms), while slow RT (within the range of 700 and 1500 ms) dominated when the target was the small item. When the target was the medium size square, RT occupied an intermediate position. In order to investigate the effects of the manipulated factors on the most representative value of the distributions, the grouped proportions at the maximal peak of each distribution was entered a multivariate extension of the nonparametric Q' analysis [34] with the hemisphere (left *vs.* right), the hemifield (nasal *vs.* temporal) and the target size (big, intermediate and small) as factors. Only the main effect of target size revealed significant ($Q'(2) = 11.1$; $p < 0.004$). Indeed, as it can be seen in Fig. 4, regardless of the hemisphere and the stimulated hemifield, RT were distributed in a similar way, with the maximal peak getting smaller with decreasing target size. The overall distribution was characterized by a peak of frequency at about 21% of all responses for big targets, 19% for medium targets, and 17% for small targets. It is noteworthy that increased RT with decreasing target size did not coincide with a general shift of the whole distribution towards larger RT values, neither with a larger spread of the distribution as it might by expected on the basis of more classic models of decision making. RT increment with decreasing target size is thus attributable to lower proportion of fast responses, a clear marker of attention-related processing [35]. This last finding is of fundamental interest because it suggests that, in addition to speeded processing, the amount of fast responses is increased when the most salient item of the display gains priority.

2.2.4. Accuracy

The proportion of correct responses ranged from 0.52 to 0.92 (mean: 0.71 ± 0.09). ANOVA was carried out on the proportion of correct responses, with the hemisphere (left *vs.* right), stimulated hemifield (nasal *vs.* temporal) and target size (big, medium, small) as within-subject factors. The main effect of hemisphere was significant ($F(1,39) = 12.65$; $p < 0.001$), with accuracy being greater for the LH (0.73) than RH (0.70), which is consistent with the fine-grained

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[4] $\alpha = \text{covariance}(x,y)/\text{variance}(x)$ where x is the surface of each of the three squares in mm^2 and y is the RT when each square was the target.

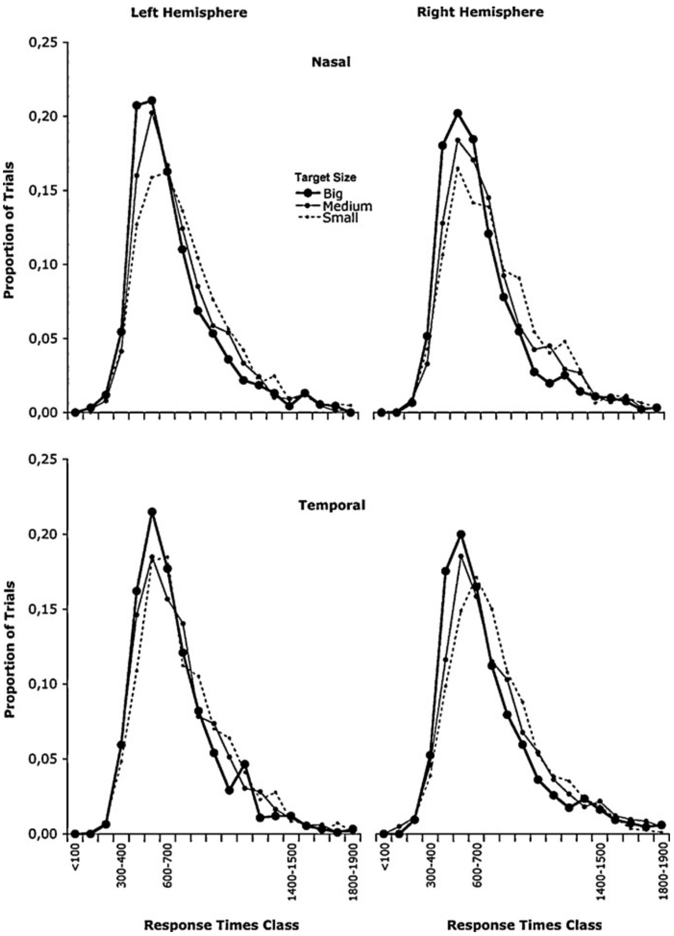

Fig. 4. Response Times distributions as a function of the target size, the stimulated hemifield and the hemisphere to which the stimuli were projected. Note that the effect of target size is not a shift of the distributions along the horizontal axis, but a decrement of the maximum peak.

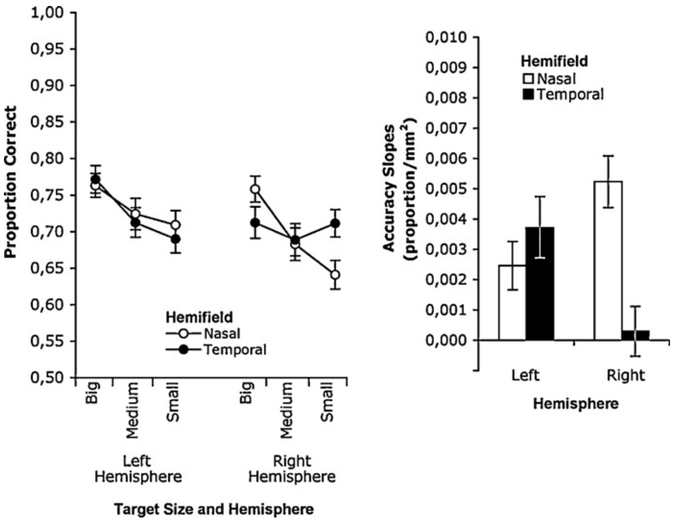

Fig. 5. (Left) Mean Proportion of correct responses (±1SEM) observed in Experiment 1 plotted as a function of the target size, stimulated hemifield and the hemisphere to which the stimuli were projected. (Right) Mean Accuracy Slopes (±1SEM) in proportion per additional square millimeter observed in Experiment 1 as a function of the stimulated hemifield and the hemisphere to which the stimuli were projected. The positive slopes indicate that each time the target would be 1 mm^2 bigger, accuracy would be better. The more the slope is near 0, the least the effect of target size on the fineness of processing.

processing of the LH [33]. The main effect of target size was also significant ($F(2,78) = 17.25$; $p < 0.00001$), with the proportion of correct responses largest when the target was the big square (0.75), smaller when it was the medium square (0.70) and smallest when it was the small square (0.69). The hemisphere × target size interaction was not significant ($F(2,78) = 0.21$; $p > 0.81$), but the effects of target size were different for nasal (0.76; 0.70; 0.67, respectively) and temporal (0.74; 0.70; 0.70, respectively) displays, as apparent from the size × hemifield interaction ($F(2,78) = 3$; $p < 0.05$). The three-way hemisphere × hemifield × target size interaction was highly significant ($F(2,78) = 9.22$; $p < 0.0003$; Fig. 5, left). Temporal-nasal asymmetries in progression are therefore different in the case of each hemisphere. To investigate this issue further, partial ANOVAs were carried out for each hemisphere, with the hemifield and target size as within-subject factors. For LH performance, only the main effect of target size attained significance ($F(2,78) = 10.9$; $p < 0.001$); the proportion of correct responses obtained was largest when the target was the big square (0.77), smaller when it was the medium square (0.72), and smallest when it was the small square (0.70). It is interesting that the hemifield × target size interaction was far from significant ($F(2,78) = 0.61$; $p > 0.544$). As can be noted from Fig. 5, the performance for the three target sizes was very similar between the nasal and temporal hemifields. This was not the case for RH performance. Once again, the main effect of target size was reliable ($F(2,78) = 11.6$; $p < 0.001$; big: 0.74; medium: 0.69; small: 0.68), but the hemifield × target size interaction was highly significant ($F(2,78) = 11.6$; $p < 0.001$). Fig. 5 shows how performance varied with target size for nasal field displays (big: 0.76; medium: 0.68; small: 0.64), but was stable for temporal field displays (big: 0.71; medium: 0.69; small: 0.71). Furthermore, Newman–Keuls post hoc comparisons revealed that performance was weaker for temporal field displays than for nasal field displays in respect of big targets ($p < 0.021$), but better for temporal displays than for nasal displays in respect of small targets ($p < 0.001$). No nasal–temporal asymmetry was found for medium targets ($p > 0.72$). Finally, it is important to note that big target performance was better than small target performance in LH nasal ($p < 0.029$), LH temporal ($p < 0.0003$) and RH nasal fields ($p < 0.0002$), but not in the RH temporal field ($p > 0.99$).

2.2.5. Accuracy slopes

Once again, the overall performance as a function of the target size almost perfectly fit a linear function with respect to the surface of the target in mm^2 (mean determination coefficient $r^2 = 0.908$), an analysis of progression slopes (α) expressed in accuracy gain per additional square millimeter served to investigate the progression further. In general, independently of the hemisphere and hemifield, the progression slope was 0.29%/mm^2, with 75% of subjects exhibiting such a positive slope ($p < 0.001$ binomial). In other words, for each additional square millimeter subjects discriminate the target orientation ≈0.3% better. This global slope was reliably different from 0 ($t(39) = 4.97$; $p < 0.00001$), as was the left nasal slope (0.25%/mm^2; $t(39) = 3.1$; $p < 0.0036$), left temporal slope (0.37%/mm^2; $t(39) = 3.6$; $p < 0.0009$), and right nasal slope (0.52%/mm^2; $t(39) = 6.12$; $p < 0.00001$). The right temporal slope did not differ from 0 (0.03%/mm^2; $t(39) = 0.37$; $p > 0.71$). These progression slopes were subjected to an ANOVA, with the hemisphere (left *vs.* right) and hemifield (nasal *vs.* temporal) as within-subject factors. There was a significant main effect of hemifield ($F(1,39) = 5.43$; $p < 0.025$), with shallower progression slopes for displays presented in the temporal (0.20%/mm^2) hemifield than for those presented in the nasal (0.38%/mm^2) hemifield. The hemisphere × hemifield interaction was significant ($F(1,39) = 13.82$; $p < 0.0006$; Fig. 5, right). Newman–Keuls *post-hoc* comparisons showed no nasal–temporal asymmetry in the LH ($p > 0.29$), but a well-marked asymmetry was found in the RH ($p < 0.001$). Furthermore, the right temporal slope was much shallower than the left temporal slope ($p < 0.017$). Overall, shallower slopes were observed for temporal displays than for nasal displays in 90% of subjects ($p < 0.0001$ binomial). When examined in respect of each hemisphere, this asymmetry was found in the RH (87.5%; $p < 0.0001$ binomial), but not the LH (47.5%; $p > 0.43$ binomial). Thus, compared with the LH, the marked RH nasal–temporal asymmetry was well confirmed and fairly regular across subjects. Similar results were obtained when progression slopes were computed as a function of the stimulus angular size (main effect of hemifield $F(1,39) = 5.58$; $p < 0.024$; and hemisphere × hemifield interaction $F(1,39) = 14.0$; $p < 0.0006$) or luminance (main effect of hemifield $F(1,39) = 6.58$; $p < 0.015$; and hemisphere × hemifield interaction $F(1,39) = 14.64$; $p < 0.0005$).

Correlation coefficients between RT slopes and accuracy slopes were computed. Interestingly, there was no correlation for LH nasal ($r(38) = -0.1$; $p > 0.53$), LH temporal ($r(38) = -0.04$; $p > 0.82$), RH nasal ($r(38) = -0.17$; $p > 0.29$), nor RH temporal ($r(38) = -0.1$; $p > 0.53$). This suggests that these two measures rely on different mechanisms [36].

With brief exposure, efficient processing depends on directing attention towards the target on either the first or one of the first deployments. In Experiment 1, where there was no incentive to direct attention towards a particular stimulus, the chance of deploying to the target first was 33%. It was demonstrated that, as the difference between one item and its neighbors increased, the chance of deploying to that item also increased and, naturally, the chance of deploying to the other items decreased. Consequently, if the first item to which attention was deployed was the target, the search would end soon afterwards, but if it was not, attention would deploy to the second most salient item, and so on. This seems to be a general principle for RT, insofar as subjects were faster to respond when the most salient item of the display was the target, and RT increased as target salience decreased. This was confirmed with the RT distribution analysis, which showed peak decrements with decreasing target size. Furthermore, the extent of the expected ordered pattern was similar regardless of which hemisphere was stimulated. An initial conclusion that can be drawn here is that the result of processing taking place within the input pathways – the geniculate and extrageniculate – and being relayed to cortical attention-related areas [37] provides enough information to allow attention to be deployed in a salience-based fashion [2]. More specifically, information at least about the location and size of each object is conveyed via each pathway and within as little as 100 ms (the display duration used here), since the former is essential for locating items in space and the latter for determining their salience (in the present study). Analysis of the progression slopes proved interesting in that it revealed a rather satisfactorily regular superiority of the temporal hemifield, since 65% of subjects exhibited shallower slopes in the temporal hemifield, regardless of which hemisphere was stimulated. This regularity failed, however, to provide significant results on shallower slopes overall. If, as previously said, shifts of attention were generated by the same network whatever the input, this finding suggests that, in many subjects, attention shifted more quickly from one item to the next when stimuli were directed to the temporal hemifield and partly supplements previously reported nasal–temporal asymmetries in attention [38–41]. Nonetheless, if we adopt the view that temporal field superiority reflects extrageniculate functioning [18,23], then our results argue against the hypothesis that the extrageniculate pathway only conveys information faster than the geniculate pathway, because in this case it would mean that overall RT is faster in the temporal hemifield whereas progression slopes are the same. Consequently, these results do not support the existence of a slightly asynchronous transmission of visual signals that help establish the hierarchy of salience within the cortical networks.

A careful analysis of accuracy produced several interesting results. First, the overall decline in performance with size decrement was shallower in the temporal hemifield than the nasal hemifield, as found in raw accuracy and accuracy slopes. Furthermore, this effect was highly regular insofar as it was shown by 90% of subjects. However, as shown by the analysis of raw accuracy, accuracy slopes and frequency effects, if account is taken of hemispheric patterns no such nasal–temporal asymmetry was found in the LH. Conversely, the same analyses revealed a striking nasal–temporal asymmetry in the RH. In fact, performance slumped as a function of target size for nasal displays, whereas there was no drop in performance at all in the case of temporal displays where slopes did not differ from 0, and it is all the more interesting that mean performance was similar between the two fields. If accuracy is a direct reflection of the detailed target analysis, a shallower progression may reflect analysis of the current item, which may be independent from its salience. The fact that accuracy did not improve in the RH temporal, despite such an improvement in RT, does suggest that the analysis of the item currently being considered is separate from its salience. An alternative and opposite interpretation is that the hierarchy of salience is so strong that the deployment of attention from the most to the least salient item happens so quickly that accuracy remains high. However, if this interpretation were correct, performance should be higher for all three items in the temporal hemifield when compared with the nasal hemifield, whereas instead it was lower for the most salient item and almost identical for the intermediate item. This alternative interpretation can thus be dismissed. A last alternative is that when presented in the temporal hemifield and directed to the right hemisphere, each stimulus is processed independently from the others and, as such, there would be no need for a hierarchy of salience to be established. The three stimuli would be processed simultaneously resulting in the invariable accuracy observed as a function of the stimulus size. However, this is a general hypothesis and should also hold for processing speed. Therefore, RT should not vary as a function of the target size either. Instead, we found that RT did vary. This third alternative can also be ruled out. To the best of our knowledge, this is the first time a marked nasal–temporal asymmetry has been found in a task combining salience-based deployments of attention and fine perceptual discrimination. In fact, a previous study by our laboratory failed to demonstrate such asymmetry in a visual search task where the physical similarity between the target and its neighbors varied parametrically [41].

The results of Experiment 1 can thus be summed up as follows: the fact of simultaneously presenting three items that are slightly different in size (1) produces effects of attentional capture since subjects processed the most salient item more quickly and, on the whole, more accurately; (2) produces an almost linear progression of both RT and accuracy as a function of the target surface, starting from the most salient item and ending with the least salient item. This was the result to be most expected since it indicates a salience-based progression of visual attention; (3) a salience-based progression of attention seems to take place whether stimuli are projected to the nasal or the temporal hemifield, and whether they are directed towards the left or right cerebral hemisphere; (4) the deployment of visual attention is fairly regularly accelerated when stimuli are projected to the temporal hemifield, which suggests that the hierarchy of salience is somewhat stronger, rendering items more distinct from each other. However, such a conclusion should be moderated since the overall slopes did not differ between the hemifields; (5) when items are processed preferentially by the RH, the salience-based accuracy improvement is apparent only if stimuli are directed to the nasal hemifield, and no signs of such a progression are found in the temporal hemifield, which may imply that the analysis of the item in question is separate from its salience. No nasal–temporal asymmetry was found in respect of displays processed by the LH; and, finally, (6) an overall superiority of the LH was found in both RT and accuracy, which is in keeping with the LH's fine-grained visual processing.

3. Experiment 2: salience or physical strength?

There are some potential objections however as to how the results observed in Experiment 1 are to be interpreted. Does the progression pattern observed in both RT and accuracy reflect a salience-based progression of attention or does it reflect easiest processing as a function of target size? It is a fact that a large item is more visible and brighter than the other items and can be processed faster. In addition, the visibility of the small gap – that determines the response – may depend on the size of the square on which it is located, even though it is physically identical in all three items. If such were the case, presenting at least the big and the small squares alone under conditions that were otherwise the same as in Experiment 1 should yield effects and interactions that are just as strong as before. Such a result would challenge the attentional account and favor a purely sensory explanation [9], in that the aforementioned nasal–temporal asymmetries would merely reflect straightforward sensory differences, like different neuronal transmission speeds or different degrees of visual analysis. Experiment 2 was carried out to investigate this alternative.

3.1. Materials and methods

3.1.1. Subjects

The same as in Experiment 1.

3.1.2. Stimuli and apparatus

The stimuli were the big and the small squares used in Experiment 1. Each had a 3-pixel gap and was rotated 0° or 180° clockwise. The squares were presented singly to the left or right of fixation, at a distance of 3.8°.

3.1.3. Procedure

The procedure was similar to the one used in Experiment 1 with the difference that the display contained a single square, a big or a small. Each subject completed a 30-trial training session, followed by an experimental session consisting of 360 trials (30 trials/search display location/target size/eye).

3.2. Results

Five subjects (12.5%) made no errors. They were therefore excluded from the analyses for ceiling effects not to contaminate the data.

3.2.1. Response times

Response times of less than 100 ms and more than 2000 ms were discarded as errors of anticipation and inattention, respectively. Less than 0.03% of the trials fell into these categories and were thus discarded. An ANOVA was carried out on the correct RT, with hemisphere (left *vs.* right), stimulated hemifield (nasal *vs.* temporal) and target size (big *vs.* small) as within-subject factors. The main effects of hemisphere (LH: 430 ms; RH: 433 ms; $F(1,34) = 0.47$; $p > 0.49$) and hemifield (nasal: 429 ms; temporal: 434 ms; $F(1,34) = 1.09$; $p > 0.30$) failed to attain significance. Of most interest is the lack of any main effect of target size ($F(1,34) = 0.02$; $p > 0.89$), with RT being similar for big (432 ms) and small (431 ms) targets. No significant effects were found for the hemisphere × hemifield interaction ($F(1,34) = 0.95$; $p > 0.33$), the hemisphere × target size interaction ($F(1,34) = 0.91$; $p > 0.34$), the hemifield × target size interaction ($F(1,34) = 2.08$; $p > 0.15$) or the hemisphere × hemifield × target size interaction ($F(1,34) = 1.75$; $p > 0.19$).

Table 1

Mean Response Times (and standard deviation) in milliseconds and mean proportion correct (and standard deviation) obtained in Experiment 2 as a function of the target size, the stimulated hemifield and the cerebral hemisphere to which the stimuli were projected.

	Left hemisphere		Right hemisphere	
	Big target	Small target	Big target	Small target
RT				
Nasal	434 (82)	429 (72)	428 (73)	425 (80)
Temporal	423 (79)	434 (87)	442 (76)	438 (78)
Accuracy				
Nasal	0.950 (0.07)	0.947 (0.08)	0.961 (0.08)	0.955 (0.07)
Temporal	0.954 (0.06)	0.946 (0.08)	0.932 (0.09)	0.936 (0.08)

3.2.2. Accuracy

The mean individual proportion of correct responses ranged from 0.78 to 0.99 (mean: 0.95 ± 0.05). ANOVA was carried out on the proportion of correct responses with the hemisphere (left *vs.* right), the stimulated hemifield (nasal *vs.* temporal) and the target size (big *vs.* small) as within-subject factors. The results reflected those of RT. The main effects of hemisphere (LH: 0.95; RH: 0.95; $F(1,34) = 0.09$; $p > 0.77$) and hemifield (nasal: 0.95; temporal: 0.94; $F(1,34) = 0.95$; $p > 0.33$) failed to reach significance. Importantly, the main effect of target size failed to reach significance ($F(1,34) = 0.17$; $p > 0.68$), with accuracy as good for big targets (0.949) as for small (0.946). There was no evidence of significant effects for the hemisphere × hemifield interaction ($F(1,34) = 2.14$; $p > 0.15$), the hemisphere × target size interaction ($F(1,34) = 0.15$; $p > 0.69$), the hemifield × target size interacion ($F(1,34) = 0.04$; $p > 0.83$) or the hemisphere × hemifield × target size interaction ($F(1,34) = 0.55$; $p > 0.46$) (Table 1).

3.3. Discussion

In Experiment 1, an ordered pattern was evidenced in respect of both chronometric performance and accuracy. Subjects responded faster and more accurately when the target was the largest of three briefly, simultaneously and laterally presented items, more slowly and less accurately when it was the medium-sized item, and even more slowly and less accurately in the case of the smallest item. Can the physical strength (size and luminance) of those stimuli fully account for such a pattern? The results of Experiment 2 are sufficiently clear to allow such a hypothesis to be ruled out. Subjects responded as quickly and accurately to the largest item as the smallest when each was presented singly. This is in stark contrast to the results of Experiment 1 when the stimuli were presented together. It is interesting that the differences previously found in accuracy as a function of hemifield and hemisphere were no longer observed, which runs counter to how those results were interpreted in terms of pure sensory effects. For the pattern of Experiment 1 to occur, several competing items have to be present simultaneously and must differ in at least one dimension; this is exactly what defines salience. One of the most interesting findings in Experiment 2 is perhaps the absence of nasal–temporal asymmetry, whether or not the stimulated hemisphere is taken into account. This absence cannot be due to ceiling effects insofar as nasal–temporal asymmetries have been reported with easier tasks, such as spatial cueing (e.g., [40]) and attentional capture [30], and insofar as another research project failed to reveal such asymmetries in a search task with varying degrees of difficulty [41].

4. Experiment 3: replication of Experiment 1

The results of Experiment 1 showed a surprising dissociation between response speed and response accuracy, which was confined to displays projected to the right cerebral hemisphere. Current models (e.g. [42]) for two-choice decisions – as the decisions made by subjects in the present series of experiments – do not assume such dissociations. By contrast, they assume that a single decision threshold links response speed and response accuracy. On the basis of such models, it would be expected that when attention is deployed to a stimulus, discrimination should be better and faster. This was also our initial hypothesis. So, we are facing two possible alternatives. Either such dissociations between response speed and response accuracy are possible [36] and they just reflect the function of distinct underlying systems – in which case, they cannot be accounted for by global models of performance (e.g. [42]) because such models were not proposed at this aim – or we face an experimental bias and we need to replicate the results. The aim of Experiment 3 was to replicate the results of Experiment 1 by targeting the effects of interest, among which the RT/accuracy dissociation.

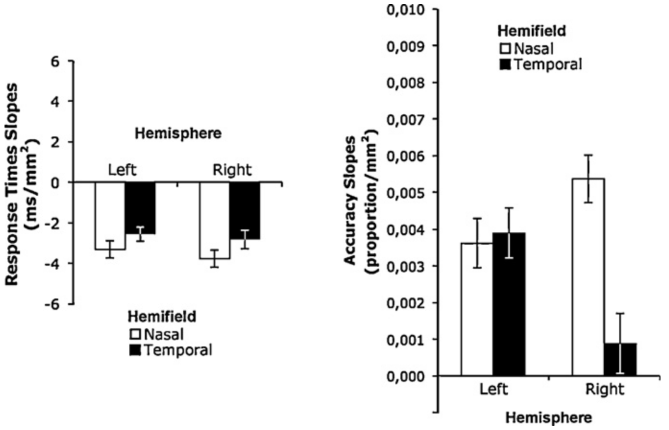

Fig. 6. Combined results of Experiments 1 and 3 depicting progression of performance per additional square millimeter as a function of the stimulated hemifield and the hemisphere to which the stimuli were projected. (Left) Mean Response Times Slopes (±1SEM) in milliseconds per additional square millimeter. (Right) Mean Accuracy Slopes (±1SEM) in proportion per additional square millimeter.

4.1. Materials and methods

4.1.1. Subjects

Thirty-four healthy volunteers, 7 males and 27 females, took part for course credits. Their mean age was 22.1 ± 2.8 years; they were all right-handed according to the Edinburgh laterality inventory (mean laterality: 0.86 ± 0.13; [32]), all had normal or corrected-to-normal vision, and were not under any medication. They all gave their written consent for their participation.

4.1.2. Stimuli, apparatus and procedure

The same as in Experiment 1.

4.2. Results and discussion

4.2.1. Response times and response time slopes

Response times smaller than 100 ms and larger than 2000 ms were discarded as representing errors of anticipation and inattention, respectively. This exclusion accounted for less than 0.6% of the trials. ANOVA was performed on the mean correct RT with the hemisphere (left *vs.* right), stimulated hemifield (nasal *vs.* temporal) and target size (big, medium, small) as within-subject factors. Only the main effect of target size was significant ($F(2,66) = 45.9$; $p < 0.00001$). RT were faster when the target was the big square (682 ms), slower when it was the medium square (721 ms), and slowest of all when it was the small square (751 ms). The overall progression slope ($-3\,\text{ms/mm}^2$) was highly different from 0 ($t(33) = 7.8$; $p < 0.0000001$) and 94.1% of subjects exhibited such a negative slope ($p < 0.00001$ binomial). Significantly negative slopes were found in all four tested conditions (LH nasal, $p < 0.00003$; LH temporal, $p < 0.000002$; RH nasal, $p < 0.00001$; and RH temporal, $p < 0.0001$). Yet, the progression slope was marginally shallower for temporal ($-2.6\,\text{ms/mm}^2$) than nasal ($-3.3\,\text{ms/mm}^2$; $t(33) = 1.67$; $p < 0.053$), and this pattern was exhibited by 67.6% of subjects ($p < 0.029$ binomial).

4.2.2. Accuracy and accuracy slopes

ANOVA was carried out on the proportion of correct responses, with the hemisphere (left *vs.* right), stimulated hemifield (nasal *vs.* temporal) and target size (big, medium, small) as within-subject factors. The main effect of hemisphere was marginally significant ($F(1,33) = 3.64$; $p < 0.065$), with accuracy being greater for the LH (0.68) than RH (0.66). The main effect of target size was significant ($F(2,66) = 33.21$; $p < 0.00001$), with the proportion of correct responses being largest when the target was the big square (0.72), smaller when it was the medium square (0.69) and smallest when it was the small square (0.62). Indeed, the overall progression slope ($0.4\%/\text{mm}^2$) was significantly different than 0 ($t(33) = 5.96$; $p < 0.000001$), with 88.2% of subjects exhibiting such a positive slope ($p < 0.00001$ binomial). As in Experiment 1, partial ANOVAs were carried out for each hemisphere, with the hemifield and target size as within-subject factors. For LH performance, only the main effect of target size attained significance ($F(2,66) = 31.9$; $p < 0.00001$); the proportion of correct responses obtained was largest when the target was the big square (0.73), smaller when it was the medium square (0.70), and smallest when it was the small square (0.62). The progression slope was $0.45\%/\text{mm}^2$ ($t(33) = 6.2$; $p < 0.000001$). The hemifield × target size interaction was not significant ($F(2,66) = 0.21$; $p > 0.81$). For RH performance, the main effect of target size was reliable ($F(2,66) = 17.4$; $p < 0.0001$; big: 0.71; medium: 0.67; small: 0.62), as well as the hemifield × target size interaction ($F(2,66) = 3.8$; $p < 0.028$). The effects of target size were more pronounced for nasal field displays (big: 0.74; medium: 0.69; small: 0.60) than temporal field displays (big: 0.67; medium: 0.66; small: 0.64). The progression slopes of the two hemifields were significantly different (nasal: 0.55%/mm2; temporal: 0.16%; $t(33) = 1.97$; $p < 0.028$), and only that of the nasal hemifield was significantly different from 0 ($t(33) = 5.47$; $p < 0.00001$). In the temporal hemifield, performance did not progress as a function of the target size ($t(33) = 1.03$; $p > 0.31$).

Despite some differences most probably due to sample characteristics, the results of Experiment 3 are sensibly similar to those obtained in Experiment 1. The progression of performance as a function of the target size was obtained once more in both RT and accuracy. Furthermore, a dissociation was observed between RT and accuracy for displays projected to the right hemisphere, mainly due to the presence of a nasal–temporal asymmetry in accuracy. Consequently, we combined the results of these two experiments (Fig. 6) in order to gain statistical strength because of the important sample size ($n = 74$) and investigated the two points that could have been controversial: the nasal–temporal asymmetry in RT progression slopes and the nasal–temporal asymmetry in accuracy progression slopes for stimuli projected to the right hemisphere. First, an ANOVA was carried out on RT progression slopes with the hemifield (nasal *vs.* temporal) and the hemisphere (LH *vs.* RH) as within-subject factors. The main effect of hemifield reached significance ($F(1,73) = 6.3$; $p < 0.015$; Fig. 7 left) with attention progressing faster for displays projected in

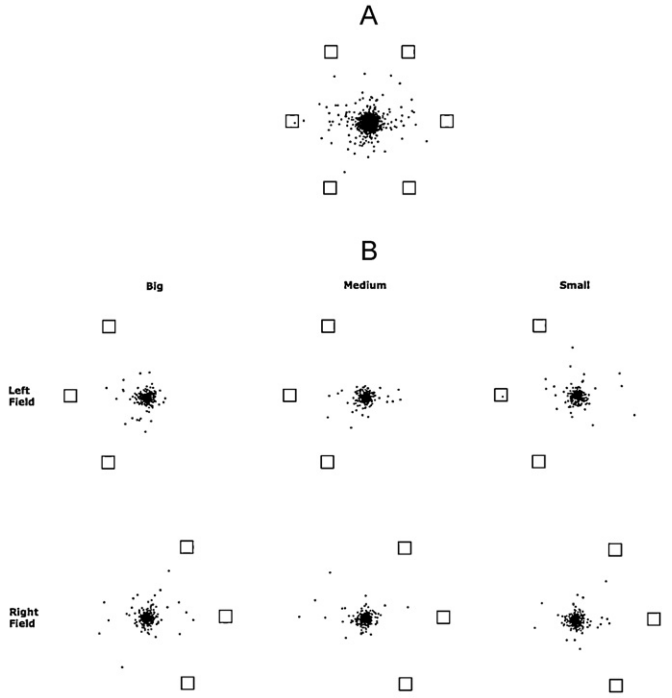

Fig. 7. Position of the eyes in the 100th ms of stimulus presentation as recorded in the control Experiment independently of the target size and field of presentation (A), and as a function of the target size and field of presentation (B).

the temporal (-2.7 ms/mm^2) than the nasal (-3.5 ms/mm^2) hemifield, a regular effect (66.2% of subjects; $p < 0.0035$ binomial). This suggests that the marginal effects observed in both Experiments 1 and 3 were merely due to statistical power. Second, an ANOVA was carried out on accuracy progression slopes with the hemifield (nasal *vs.* temporal) and the hemisphere (LH *vs.* RH) as within-subject factors. The hemifield × hemisphere interaction was highly significant ($F(1,73) = 12.1$; $p < 0.0008$; Fig. 7, right). The nasal–temporal asymmetry in accuracy found for left-sided (RH) displays was confirmed through Newman–Keuls *post-hoc* analyses ($p < 0.0001$) since performance progressed as a function of the target size in the nasal hemifield (0.54%/mm^2) but not in the temporal hemifield (0.09%/mm^2). No such asymmetry was found for right-sided (LH) displays ($p > 0.75$; nasal hemifield: 0.36%/mm^2; temporal hemifield: 0.39%/mm^2). These results confirm the existence of a nasal–temporal asymmetry in the salience-based progression of attention.

One of the most powerful models of human performance in situations of two-choice decisions [42] proposes that a single decision threshold links response speed and response accuracy. Discrimination should be better whenever response speed increases, and *vice versa*. The results of Experiments 1–3 showed that the salience of a stimulus relatively to its immediate neighbors, not its mere size or luminance, attracts attention and, consequently, globally speeds response time and increases accuracy. Indeed, taken independently of hemisphere and visual hemifield, salience-based progression is found in both RT and accuracy, and this is in agreement with decision-making models [e.g., 42]. Yet, these are global models of performance and do not really envisage the probability that such coherence between speed and accuracy might rise because of the combined action of distinct neural subsystems, each one having different properties and obeying to different laws of functioning. The results of Experiment 3 mostly replicate those of Experiment 1 and, in agreement with previous studies [36], suggest that dissociations between RT and accuracy are possible. Of course, this does not run counter the psychophysical models of performance since, in general, they are not designed to account for differences in the functioning of distinct neural pathways.

5. Experiment 4: Do the eyes move towards the target within 100 ms?

Even though in Experiments 1 and 3 the stimulus display was presented very briefly (i.e., 100 ms) there is a slight probability that subjects were able to move their eyes towards the target before its extinction. In such a case, any systematic differences between conditions could mask any interesting results and compromise our interpretations in terms of covert orienting of attention. We therefore conducted a control Experiment during which eye movements were recorded. The setting was identical to the one used in Experiment one except that subjects participated under binocular viewing conditions because of technical constraints. Here, we present only a summary description of the eye tracking data, confined to the position of the subjects eyes at the 100th millisecond of the stimulus display (i.e., just before its disappearance). We show that subjects cannot foveate any item, be it the target or not, within 100 ms. Analyses of behavioral data are also reported, based on the effect of target size.

5.1. Materials and methods

5.1.1. Subjects

Thirteen healthy volunteers, 5 males and 8 females, participated in the control Experiment. Their mean age was 23.7 ± 1.1 years; they were all right-handed, all had normal or corrected-to-normal vision, and were not under any medication. They all gave their written consent for their participation.

5.1.2. Stimuli and apparatus

The stimuli were the same as in Experiment 1. Eye tracking data were recorded with an iView X^{TM} Hi-Speed 1250 device (SensoMotoric Instruments) with an 500/1250 Hz sampling rate, an 0.2–0.5° gaze position accuracy, a tracking resolution less than 0.01°, and a processing latency of 0.5 ms. The system was controlled by E-Prime software. The sampling rate was set to 1 recording every 2 ms (i.e., 50 recordings during the 100 ms of presentation of the stimulus display).

5.1.3. Procedure

The procedure was similar to the one used in Experiment 1 with the difference that subjects participated under binocular viewing conditions. Each subject completed a 16-trial training session, followed by an experimental 216-trial session (72 trials/target size). RT and errors were recorded by the computer.

5.2. Results and discussion

5.2.1. Response times

Response times of less than 100 ms and more than 2000 ms were discarded as errors of anticipation and inattention, respectively. Less than 0.05% of the trials fell into these categories and were thus discarded. ANOVA was therefore performed on the mean correct RT with target size (big, medium, small) as the unique within-subject factors. The main effect of target size was significant ($F(2,24) = 6.35$; $p < 0.006$). RT were faster when the target was the large square (653 ms), slower when it was the medium square (710 ms), and slowest when it was the small square (715 ms). The progression slope was -2.9 ms/mm^2 and it was reliably different from 0 ($t(12) = 2.82$; $p < 0.016$).

5.2.2. Accuracy

The proportion of correct responses ranged from 0.55 to 0.78 (mean: 0.68 ± 0.08; 1908 correct trials out of 2808). ANOVA was carried out on the proportion of correct responses, with the target size (big, medium, small) as the unique within-subject factors. The main effect of target size was significant ($F(2,24) = 8.13$; $p < 0.002$), with the proportion of correct responses largest when the target was the big square (0.741), smaller when it was the medium square (0.653) and smallest when it was the small square (0.636). The progression slope was $0.49\%/\text{mm}^2$ and it differed from 0 ($t(12) = 3.84$; $p < 0.002$).

5.2.3. Eye tracking results

For the purpose of this Experiment, we present here only the position of the eyes at the 50th sampling (i.e., at the 100th millisecond of the stimulus display presentation). Out of 1908 correct trials, 70 (≈3.7%) were excluded from the analysis because of blinking, and the eye position in each of the remaining 1838 was plotted against the stimulus display. All conditions taken together (Fig. 7A), eye movements could reach a target location (3.8° of eccentricity) only in one trial out of 1838. The majority of eye movements (94.2%) was made at a radial distance of 0.7° from fixation (central movements). The remaining 5.8% of eye movements were made up to a radial distance of 2.3° from fixation (wide-spread movements). Taken separately for each hemifield and target size (Fig. 7B), eye movements were within the radial distance of 0.7° from fixation in 94.7%, 95.6% and 94.4% of trials for left field big, medium and small targets, respectively, and in 93.7%, 93.9% and 93.1% of trials for right field targets. These proportions were entered a multivariate nonparametric Q' analysis [34] with the display hemifield (left *vs.* right) and the target size (big, medium and small) as factors. The main effect of hemifield ($Q'(1) = 0.92$; $p > 0.33$), the main effect of target size ($Q'(2) = 0.44$; $p > 0.80$) and the hemifield × target size interaction ($Q'(2) = 0.09$; $p > 0.95$) failed to reach significance. These observations clearly show that target items located at 3.8° from fixation cannot be foveated with a stimulus exposure duration of 100 ms. Subjects move their eyes hardly beyond the central 0.7° and never reach the stimulus display. Furthermore, there are no systematic differences across conditions. An interesting finding is that, whatever the hemifield in which the stimulus display was presented, the ≈6% of wide-spread movements were not systematically directed towards the stimulus display. In many cases, the stimulus display was on the left of fixation and eye movements were directed to the right , and *vice versa* (see Fig. 7B). This may suggest that those movements were not meant to reach the stimulus display but were probably made at random. Else, why should subjects try to foveate a stimulus presented on the right by moving their eyes to the left? In overall, eye movements were not responsible for the differences observed across conditions in Experiments 1 and 3. Those differences reflect effects of covert attention.

6. General discussion

Local differences between adjacent items in a scene generate activities that signal how different these items are from each other. The magnitude of these differences is said to determine each item's salience [2,4], which serves in turn to order inputs for further processing [16]. In the first place, attention would be involuntarily directed towards the location of the most salient item, and would then deploy progressively towards the least salient item until a target is found. Since the early 1980s researchers have tried to locate such a complex computational process at subcortical [10,13], early cortical [2,16] and late cortical [11,43] stages of visual information processing, without however reaching a consensus. It is well known, however, that the areas subserving the orienting of attention based on salience are largely right-lateralized and involve frontal and parietal cortical areas [37]. Interestingly, the parietal representation of the locations of objects is built on retino–geniculo–striate inputs (i.e., geniculate pathway), retino–tecto–pulvinate and direct retino–pulvinate inputs (i.e., extrageniculate pathways). Furthermore, most brain areas thought to generate salience receive input from, or are part of, one or both of these pathways. It is therefore quite plausible that all structures are involved in generating visual salience, but that their relative contributions depend on the result of processing taking place in each pathway. Thus, instead of asking which brain structure generates visual salience, we looked into the contribution to salience and the salience-based progression of attention of signals conveyed along the input pathways. Our investigation was based on the assumption that nasal–temporal asymmetries reflect the properties of the visual pathways although not all neuroscientists agree on the interpretation of this asymmetry [18,20,21,24], and used the multiple salience level visual search task.

In Experiment 1 subjects viewed lateralized displays, each containing three squares of different sizes, and were asked to determine the orientation of a target. To minimize saccades towards the items, the display was presented for only 100 ms. The first interesting result is that the largest item was processed first since, overall, performance in respect of the largest item was better than for the other two. Similar results were obtained in Experiments 3 and 4. The possibility that this result may just be due to the physical differences between the stimuli (i.e., size or luminance *per se*) could be ruled out based on evidence from Experiment 2 which showed that, when presented alone, the largest item was processed as quickly and accurately as the smallest. Wright and Richard [9] proposed that it is the physical strength of the input which guides the opening of a channel of attention in a stimulus-driven fashion. The greater the physical strength, the faster the channel will open and the faster the subsequent processing. This sensory-attentional hypothesis may provide a partial explanation for some previous findings [7,9] but cannot account for the results of the present study, since Experiment 2 showed that the physical strength (size and luminance) of each stimulus is not enough to produce changes in performance. Important differences were observed in the presence of multiple competing stimuli (Experiments 1, 3 and 4), however, suggesting it is mainly the difference between the stimuli (i.e., salience) that drives attention, as predicted by theorists of salience [2,4,16], and not simply absolute physical strength (i.e., the sensory response they individually evoke). The fact that the largest item captured attention and obtained processing priority [31] even in the absence of any particular incentive to process it first is purely the result of its difference compared with other items. And this is what defines salience [2,16]. This first result is thus consistent with previous findings and some models according to which attention is first directed towards the most salient item in a given scene [2,4,6].

Of most interest is the presence of an almost linear progression of both RT and accuracy with respect to the surface of the target. This was found in Experiments 1, 3 and 4. The most salient item is processed faster and most accurately, the intermediate one more slowly and less accurately, and the least salient one even more slowly and less accurately. This result indicates that visual attention progresses in space from the most to the least salient item, and as such it corroborates several existing attention models [2,4,6]. Even though such a salience-based progression has been hypothesized [2], there is scant evidence in the literature that such might be the case [7]. The present study is thus the very first time such a progression has been clearly demonstrated. For the moment, of course, there are a number of questions about the mechanisms underlying such a phenomenon. Computations taking place within areas that process visual attributes are those used afterwards to generate salience [6]. In keeping with the fact that size is an attribute computed early on in visual information processing (areas 17–19; [44,45]) and that processing of elementary attributes is seemingly not lateralized [46,47], we observed no difference in progression between the LH and RH when taken independently of the stimulated pathway. Thus, contrary to the large right-lateralized network of stimulus-driven attention orienting [37], the computations underlying the generation of salience seem not to be lateralized. This finding ties in well with the idea that salience results from quite elementary, non-lateralized computations that merely serve to order inputs for further processing [2,4,16]. Another finding that suggests salience is generated quite early on, but also that the hierarchy of salience is established during the first stages of information processing taking place within the visual system, is the fact that their effects appear soon after the stimulus has been presented. For instance, Kean and Lambert [7] showed that these effects could occur even before the first 50 ms of stimulus processing when salience is established between 2 items, and our study suggests they are already present and robust at 100 ms when three items are presented. What early mechanism could cause salience-based progression? If anything, salience is closely linked to the presence of multiple competing stimuli and should thus be based on the combination of receptive field properties of neurons and responses to stimuli outside the receptive field. One mechanism that could produce such effects is surrounding inhibition. Responses to a stimulus within the excitatory borders of the receptive field are degraded when another stimulus is simultaneously presented in the region outside these borders. Such surrounding inhibition is known to occur within both geniculate and extrageniculate pathways [48–50].

In line with this, Experiments 1 and 3 also provided evidence of a salience-based progression of attention for displays presented to both nasal and temporal fields which rules out the possibility that the source of salience is a single input pathway or even a single brain structure, such as the pulvinar [10] or primary visual cortex [2,16]. Under usual free viewing conditions, visual inputs are simultaneously processed by both geniculate and extrageniculate pathways and, therefore, several structures seem involved in salience generation. Information about the size and location of each object would be conveyed through each pathway since, in the present study, the former is essential for determining salience and the latter necessary for orienting attention. This is not surprising since size-selective neurons have been described in the superficial layers of the SC [48,49] and the pulvinar [51], as well as in the LGB and V1 [52]. However, a somewhat regular superiority of the temporal field was observed, since 66.2% of subjects (Experiments 1 and 3 combined) exhibited shallower progression slopes, meaning that attention progressed faster from the most to the least salient item. From a cognitive perspective, this may mean activities yielded through the computation of salience could have rendered each item perceptually more distinct from the others, and the larger the between-items difference the faster the deployments of attention [53]. In that case, this temporal field superiority would be due to differences in computations that establish salience and its hierarchy.

What happens during those early stages when salience and its hierarchy are established, and what are the candidate structures? The early rise of salience effects supports assumptions that salience is established either at subcortical or early cortical levels. The latency of the magnorecipient area of the LGB is very fast (≈33 ms), and responses within early cortical areas of the visual system occur as soon as 66 ms after stimulus onset [54]. Conversely, information from the superior colliculus appears to have a major influence on dorsal stream processing through two subdivisions of the retinotopically organized inferior pulvinar (Pi; [55]), the neurons of which exhibit a mean latency of 64 ms [51]. Beyond striate cortex, the cortical areas to which these two pathways project are largely shared and concern the dorsal stream which codes spatial attributes and shows responses at approximately 70 ms post-stimulus [54]. Furthermore, there is some evidence that the signal travels through different areas of the dorsal stream very quickly. This may be the key to some early effects. For instance, the extraction and indexing of spatial information, generation of salience, and establishment of a hierarchy of salience are largely the result of early processing that may be independent from the pathway through which sensory signals are conveyed (in contrast to the strength of the hierarchy of salience). As far as the extraction of spatial information is concerned, the presence of a retinotopic organization in both the LGB [56] and pulvinar [50,57,58] indicate that such information can be extracted and processed fairly early. Furthermore, psychophysical studies suggest that up to 50% of spatial information decays within the 100 ms following stimulus presentation, and up to 80% within the first 200 ms [59]. Of course, this implies that spatial information used to locate the items is extracted quite a while before these short periods. The timing of burst in the LGB and the pulvinar, and their meeting point in the parietal cortex are consistent with findings that the salience-based progression of attention, which needs spatial information to be established [2,4,6], can already be observed within 100 ms without accuracy overall dropping dramatically. Of course, the possibility that search for the target continues beyond the presentation of the display because of some sort of iconic memory cannot be excluded. Yet, such processes cannot really explain nasal–temporal asymmetries without taking into account the input pathway. In any case, the results of Experiments 1 and 3 show that salience-based progression of attention is possible irrespective of which hemifield is stimulated, and this may be in keeping with a model which holds that many of the computations giving rise to this effect are similar and probably take place in parallel via the pathways receiving input from both the nasal and temporal hemifields.

With respect to accuracy, a very regular nasal–temporal asymmetry was observed which depended on which hemisphere was stimulated. In the LH, accuracy decreased with the decrease in the target size and no nasal–temporal symmetry was observed. When the stimuli were projected to the RH, this progression was evidenced only when the nasal hemifield was stimulated. Little signs of such a progression were found for temporal stimuli. Yet, the RT analysis showed there was a salience-based progression. A key to understanding this discrepancy is the possible lack of link between the RT and accuracy progression slopes, which suggests that the mechanisms underlying RT and accuracy are not the same [36]. Intuitively, RT in each condition reflect the threshold above which each subject judged that he/she had received enough input to give an accurate response. If RT increased with decreasing target size, it is because the required input reached this threshold sooner for the biggest target, later for the medium target, and later still for the smallest target. This is compatible with a progressive deployment of attention from the most to the least salient item of the display. Unlike RT, accuracy reflects the fineness with which an item is processed, and its relative progression may reflect the degree to which analysis depended on the target salience. The striking right-lateralized nasal–temporal asymmetry in the progression of accuracy suggests that fine visual analysis did not follow the fast salient-based deployments of attention, especially for temporal displays without, however, overall accuracy to be affected. Despite being visited first, the most salient item was not processed better than the least salient one. One possible explanation is that signals conveyed to the RH – probably along the extrageniculate pathway – contain enough information to build salience and determine the processing order, but not enough to allow for fine perceptual analysis. That the spatial resolution of the RH is lower than that of the LH [33], and that performance of the RH can remain virtually unchanged while that of the LH undergoes dramatic changes [41] are not new findings *per se,* but that this may be attributed to at least the extrageniculate pathway is quite new. Such a hemispheric specialization at the subcortical level had already been suspected [60] but not demonstrated. The difference in progression patterns between RT and accuracy suggests that efficient orienting to a salient target does not necessarily mean fine processing of that target and is a striking corroboration that salience is built and guides attention with no need for fine-grained visual analysis. The absence of progression suggests that the analysis of the given item is independent of its salience when the signal it generates are conveyed to the RH through the fibers receiving inputs from the temporal hemifield. In a previous study, Michael and Desmedt [61] showed that items appearing at the same time as a target were not processed by patients suffering from lesions involving the pulvinar (mainly of the right hemisphere). The authors proposed that processing of multiple items surrounding a target was carried out by means of coarse pointers which established salience by spotting the area to select and process. The combination of pulvinar coarse pointers and the more precise pointers of the striate cortex [62], they proposed, generated spatially very precise spikes of activity surrounded by coarsely defined patterns of activity representing, respectively, the location of the most salient item and that of those in the immediate surroundings. The lack of any progression in respect of accuracy when the temporal hemifield transmits signals to the RH may support and supplement such an account in that the underlying pathway spots the location containing items to process, establishes a hierarchy of salience and differentiates each signal, allowing attention to progress in a salience-based fashion, but not allowing any qualitative difference in how each attended item is processed. This of course means the existence of functionally different computations at least for stimuli presented in the temporal hemifield and projected to the right hemisphere.

7. Conclusion

Using a new paradigm where several items of slightly different size were presented, our study shows for the very first time that attentional capture by the most salient item is followed by a progression pattern towards the least salient item. The attentional nature of these effects is evidenced by the decrement of the RT distribution peak, the fact that the least and most salient items trigger similar performance when presented alone, but also from the fact that no overt movements of attention towards the stimulus display are possible during the short time it is presented. Both cerebral hemispheres and both visual pathways have a role to play in generating salience and establishing the hierarchy of salience that helps attention progress through space. If, as suggested by some scientists, nasal–temporal asymmetries reflect differential involvement of the geniculate and the extrageniculate pathways, then the results suggest differential processing through these pathways. Attention-related areas in the parietal cortex receive inputs from both geniculate and extrageniculate pathways and build and carry out those processes accordingly. Our findings reflect the result of the processing within the same cortical network of attention and based on the same visual input, which could be processed differently along two distinct pathways. So, whatever the result of the processing taking place in each visual pathway, what is reflected through performance is how the output of these pathways is used to build salience and a hierarchy thereof. And if performance shows there are differences between nasal and temporal hemifields it is because their output, in terms of the common cortical network of attention, is not the same.

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