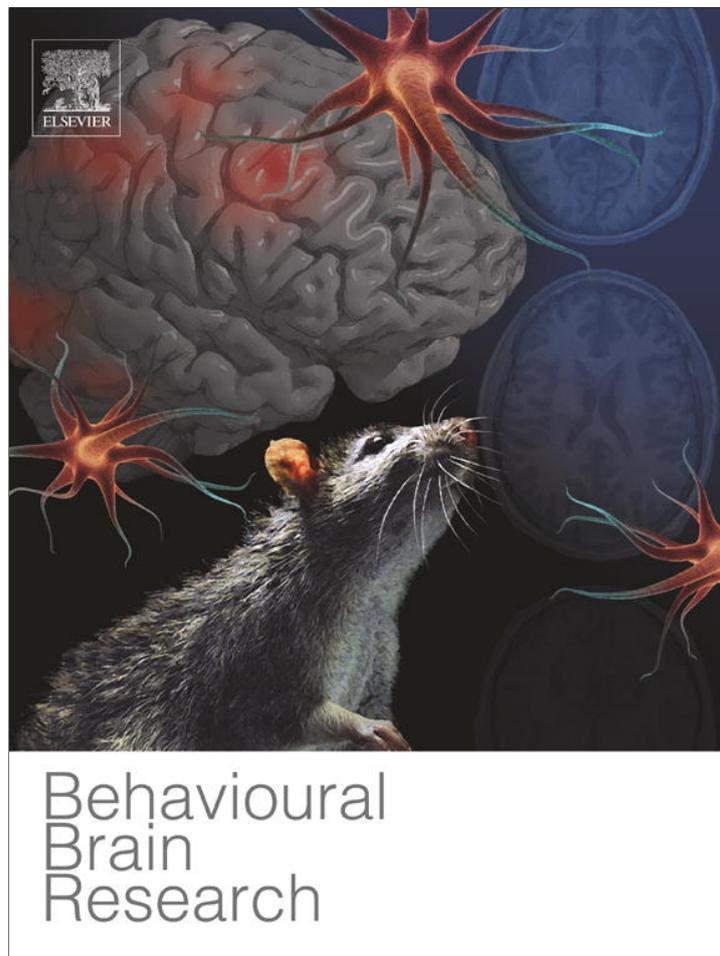


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## Review

## Two cognitive and neural systems for endogenous and exogenous spatial attention

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## HIGHLIGHTS

- ▶ Endogenous and exogenous spatial attention can be behaviorally dissociated.
- ▶ They are implemented in overlapping although partially segregated brain circuits.
- ▶ They constitute two independent attentional systems.

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## ABSTRACT

Orienting of spatial attention is a family of phylogenetically old mechanisms developed to select information for further processing. Information can be selected via top-down or endogenous mechanisms, depending on the goals of the observers or on the task at hand. Moreover, salient and potentially dangerous events also attract spatial attention via bottom-up or exogenous mechanisms, allowing a rapid and efficient reaction to unexpected but important events. Fronto-parietal brain networks have been demonstrated to play an important role in supporting spatial attentional orienting, although there is no consensus on whether there is a single attentional system supporting both endogenous and exogenous attention, or two anatomical and functionally different attentional systems. In the present paper we review behavioral evidence emphasizing the differential characteristics of both systems, as well as their possible interactions for the control of the final orienting response. Behavioral studies reporting qualitative differences between the effects of both systems as well as double dissociations of the effects of endogenous and exogenous attention on information processing, suggest that they constitute two independent attentional systems, rather than a single one. Recent models of attentional orienting in humans have put forward the hypothesis of a dorsal fronto-parietal network for orienting spatial attention, and a more ventral fronto-parietal network for detecting unexpected but behaviorally relevant events. Non-invasive neurostimulation techniques, as well as neuropsychological data, suggest that endogenous and exogenous attention are implemented in overlapping, although partially segregated, brain circuits. Although more research is needed in order to refine our anatomical and functional knowledge of the brain circuits underlying spatial attention, we conclude that endogenous and exogenous spatial orienting constitute two independent attentional systems, with different behavioral effects, and partially distinct neural substrates.

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## 1. Introduction

At any given time, a huge amount of information reaches our senses. However, in order to be effective, our actions must be usually directed to a single location or object at a time. Therefore, a selective mechanism is necessary to select relevant information so that only relevant objects are deeply processed in order to respond to them in the appropriate way. This selective role has been given to attention, a mechanism that prioritizes the processing of relevant information. Attended objects are frequently processed to high levels in the system leading to conscious awareness and voluntary reactions to them. In contrast, unattended objects are not processed at this higher level and, even if a response can be given to them, it will be automatic and out of voluntary control. Thus attention has been proposed to be a pre-requisite of consciousness [1–6], although the role of attention on conscious perception is nowadays under debate [7–14]. However, in order to maintain coherent behavior in the face of a continuously changing environment, attentional processes are needed to allow for the maintenance of goal-directed behavior in spite of distracting events, while at the same time allowing for the processing of novel, unexpected events, that could be either advantageous or dangerous, in order to appropriately respond with either approach or avoidance behavior [15].

Therefore, selecting information that is relevant for our goals is crucial for coherent behavior. Most theories agree that attention can be oriented and maintained “at our will” to specific locations or objects, according to our goals and intentions. However, the ultimate outcome of this selective mechanism might become catastrophic if new objects appearing in the scene are effectively and totally ignored. For example, ignoring the sudden appearance of a dangerous agent might more than offset the benefit of maintaining the current task goal. Therefore, selective attentional mechanisms must be complemented by other mechanisms able to detect the appearance of new objects or events. Thus, an attentional mechanism orienting to external, salient stimuli, is also thought to have an important ecological role in human beings and other species, allowing animals to be sensitive to novelty and discrepancies in the scene that could mark a predator to be avoided, or prey to be approached [16].

Consequently, two modes of attentional orienting have been proposed in order to accomplish these two important goals. Orienting of attention in space is supposed to be controlled either endogenously by the system (endogenous orienting of attention, which is also known as top-down or voluntary attention), or exogenously, by external stimulation (exogenous orienting of attention or bottom-up, involuntary stimulus-driven attention). Thus spatial attention is oriented endogenously to stimuli that are relevant for the task at hand, either because the observer has an expectancy of where the relevant stimuli would appear, or given certain incentives for responding efficiently to specific non-spatial

attributes. Additionally, spatial attention can be exogenously captured by salient stimuli (such as luminance changes, onsets, or moving stimuli) even if the observer has no intention of orienting his/her attention to that object or location.

What has to be explored then is how these two processes, exogenous and endogenous orienting, are combined in order to modulate behavior in an integrated and coherent way. A common view in the field was that exogenous and endogenous orienting processes constitute two modes of orienting a single attentional system, the two forces being in a continuous dynamical competition for the control of attention [17–20]. At each moment, the winner of the competition between the endogenous and exogenous orienting determines the location or object to which attention would be directed. In this case, it is important to know the characteristics or parameters of each orienting mode, and the nature of the interaction between the two orienting mechanisms, in order to be able to determine which would win the competition in different environmental circumstances, and therefore which information will be prioritized.

A different possibility is to consider exogenous and endogenous attention as two different attentional systems, which independently modulate performance in order to accomplish the two above described objectives of accommodating the ongoing individual's goals and environmental circumstances [21,22]. In this case, it would be important to know how each attentional system modulates performance, i.e. which stages of processing are modulated by endogenous and exogenous attention. Moreover, even if endogenous and exogenous attention are proved to be independent, it has to be understood whether or not they interact, and in which circumstances they do, for the control of behavior. In case of an interaction, its functional locus (early or late in processing) and neural underpinnings have to be determined.

We consider that if two processes are the expression of the same system, they should demonstrate the same functional characteristics, which might differ quantitatively in magnitude and/or time-course, but not in their qualitative aspects (in the case of spatial attention, a qualitative aspect can be for example the sort of coordinates in which attention operates, spatial or object-based, see below). Moreover, both processes should be implemented into the same brain circuits and modulate similar stages of processing (for example perceptual, motor, or decisional). Alternatively, if two processes reflect the existence of two independent systems, qualitative functional differences should be observed. Moreover, both systems should be implemented in well differentiated brain circuits, and modulate different stages of processing. However, it is also possible that functionally independent systems interact under certain situations. In this case, we will expect to find some behavioral interactions between the systems, although the existence of a single double dissociation will prove that, despite the interactions, the systems are functionally independent. Two independent systems that sometimes interact are expected to be implemented

in partially overlapping brain regions, but with some key nodes exclusively implicated in one type of orienting.

In the next pages we will discuss the characteristics of endogenous and exogenous attention, which for a long time have been considered two different modes of controlling attention, that is, two controlling mechanisms (internal vs. external) for the same attentional operator. Although it is well established that attention can be directed to spatial locations or objects, some manipulations leading to orienting based on spatial coordinates, and others leading to orienting based on object coordinates (see e.g. [23]), in the present review, we will focus on the dissociation between endogenous and exogenous orienting based on spatial coordinates. We will review some situations in which exogenous attention is observed independently of endogenous orienting, and some other situations in which endogenous orienting modulates exogenous orienting. The behavioral review will conclude with a review of studies demonstrating that endogenous and exogenous orienting produce qualitatively different effects on information processing, suggesting the existence of two independent attentional systems that nevertheless sometimes interact for the control of behavior. We will then explore the neural systems underlying each type of orienting. First, we will review the literature on attentional orienting, which has mainly focused on endogenous attention, and point to the existence of two different dorsal and ventral fronto-parietal networks for the control of orienting and re-orienting to task relevant events, respectively. We will also describe some of the effects that core attentional regions produce upon early perceptual areas. Finally, we will present the state of the art on the different attentional networks subserving endogenous and exogenous orienting.

## 2. Endogenous and exogenous orienting mechanisms in competition or coordination for the control of attentional orienting

### 2.1. Characteristics and parameters of endogenous and exogenous orienting

In the late 1970s – early 1980s, Posner and colleagues developed the widely used “spatial cuing paradigm”, in which a spatial cue was used to direct attention before the relevant target was presented [24–28]. In their paradigm, attention could be oriented either exogenously, using a spatially non-predictive peripheral cue, or endogenously, using a spatially predictive central cue [25] (see Fig. 1). Cues could either be valid, invalid, or neutral. Valid cues orient attention to the target location, invalid cues orient attention to a non-target location, and neutral cues provide no spatial information about the location of the upcoming target. Attentional orienting produced by peripheral and central cues usually produces benefits and costs on reaction times (RTs) and accuracy. Benefits are defined as faster RTs (or better accuracy) when valid cues are compared with neutral cues, while costs refer to slower RTs (or poorer accuracy) for invalid vs. neutral cues.

It was soon discovered that orienting of attention produced by peripheral and central cues was quite different. In a highly influential paper, Müller and Rabbitt [29] demonstrated that spatial attention is oriented faster when it is directed exogenously (by using peripheral cues) than endogenously (by using central cues). Moreover, endogenous attention can be sustained for longer periods of time than exogenous attention. In fact, the effect of exogenous attention is not sustained on time, reversing at long cue-target intervals; RTs become slower at the exogenously attended location (valid location) than at the unattended location (invalid location). This effect, known as Inhibition of Return (IOR; [26,27]), has been proposed to be a mechanism that facilitates visual search, avoiding re-inspection of previously explored locations [30,31]. Peripheral cues can also be made predictive of the future

location of target appearance [32]. When peripheral cues predict target appearance at the same spatial location (i.e., predictive cues), participants have an incentive to maintain attention at the cued location. Thus, peripheral predictive cues produce both an initial exogenous attentional capture, and an endogenous maintenance of attention at the indicated location [33]. Peripheral cues can also be made counter-predictive, indicating that the target will probably appear at a different location from the cued location. In this case, participants have an incentive to remove attention from the cue to effectively attend the indicated spatial location. Their effects on behavior will be further discussed later in this review.

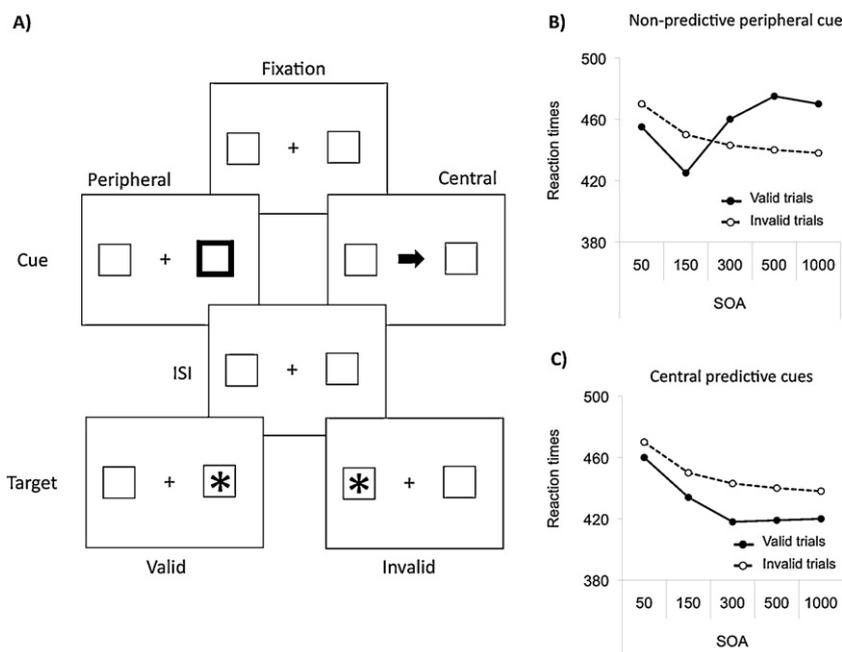
Apart from their different time course, exogenous and endogenous forms of attention have been shown to have different characteristics. For example, unlike endogenous orienting produced by symbolic central cues, the facilitatory effects of exogenous orienting produced by peripheral cues are not affected by a secondary memory task, by the information provided by the cue on where the target will appear, and cannot be voluntarily suppressed [34]. Additionally, once activated, exogenous orienting is more resistant to interference produced by other peripheral cues than endogenous orienting is [29]. Based on this data, Jonides [34] postulated that exogenous attention was more automatic than endogenous attention, which would be under voluntary control. However, it has recently been demonstrated that endogenous attention does not consist of a voluntary and effortful orienting of attention. For example, when using spatially predictive peripheral cues, similar orienting effects are observed when instructions to endogenously orient attention are given or not; and when participants are conscious of the relationship between the cue and the target or when they are not [35–39].

Concerning the relationships between endogenous and exogenous attentional orienting, Posner et al. [27] and Jonides [34] proposed that attention was a unitary mechanism that could be moved (“transported”) either exogenously or endogenously. Müller and Rabbitt [29] postulated instead that exogenous and endogenous orienting were in fact two different attentional mechanisms that “addressed the same limited-capacity attention system”, i.e., they postulated that endogenous and exogenous attention constituted separate mechanisms in competition to direct attention to the relevant location. The final product of this competition would be the measured orienting response. However, in both cases the final effect of attention would be the result of the final orienting of a unitary attentional mechanism.

### 2.2. Endogenous modulation of exogenous orienting

In the competition for the control of orienting, it has been shown that endogenous attention can modulate the effect of exogenous orienting. In this section, we will review studies that have shown how different endogenous factors modulate exogenous orienting.

One of the first pieces of evidence demonstrating that the exogenous orienting of attention is not completely automatic, and can be modulated by endogenously attending to a location in space was reported by Müller and Rabbitt [29]. They studied whether endogenous attention was resistant to the interruption produced by exogenous stimuli. They presented a spatially predictive central arrow cue followed by a target at different time intervals (600, 900, 1200 ms). In some trials, a non-predictive peripheral cue was presented 500 ms after the central cue. In order to maximize overall performance, participants should try to ignore the peripheral cue and focus attention at the location the central cue was pointing at. Their results showed that endogenous attention enhanced the effect of exogenous attention when the central and the peripheral cue indicated participants to attend at the same location. Moreover, endogenous attention attenuated the effect of exogenous attention when the peripheral cue was presented at a different,



**Fig. 1.** (A) Illustration of a typical Posner paradigm in which targets can be preceded by either peripheral or central cues. (B) Typical mean RT results observed when peripheral non-predictive cues precede targets at different SOAs. RTs are faster for valid vs. invalid trials at short SOAs, but the effect reverses at SOAs longer than 300 ms, demonstrating an IOR effect. (C) Typical mean RT results observed when central predictive cues precede targets at different SOAs. RTs are faster for valid vs. invalid trials, and the effect is sustained even at the longest SOA.

invalid, location. They speculated that endogenous attention did not directly modify the effect of exogenous attention, but the modulation occurred by strengthening the effect of exogenous attention. They concluded that the exogenous orienting mechanism was an “autonomous module that can be modified but not suppressed by endogenous attention”.

Yantis and Jonides [20] explored whether the exogenous attentional capture produced by abrupt onsets was automatic or could be modulated by endogenous attention. They demonstrated that only when a central arrow cue was completely reliable (indicating the target location with 100% validity), abrupt onsets did not capture attention when they were presented at a distracting location. However, when central cues were not 100% predictive, abrupt onset distractors did produce an effect on performance, as shown by slowed RTs to the target when the response associated to distractors was incompatible with the target's response (see also [40], for similar results using a different paradigm). As suggested by Müller and Rabbitt [29], this result might indicate that exogenous attention can be modulated, but rarely completely suppressed by endogenous attention. In other words, an interim conclusion at this point might be that exogenous attention can be automatic by default, but it can be endogenous modulated, or even suppressed under certain conditions (see [41], for a review of this issue).

In clear opposition to this conclusion is, however, the “contingent attentional capture” hypothesis advanced by Folk, Remington and colleagues [42,43], which states that only relevant stimuli can in fact capture attention. These authors have demonstrated that the exogenous capture of attention critically depends on the task set adopted for responding to the target. Using a modified version of the cuing paradigm, Folk et al. [43] demonstrated that onset cues were able to capture attention only when the participants' task was to respond to an onset-target but not when they had to respond to a color-target. Similarly, singleton-color cues only captured attention when participants had to respond to a singleton-color-target, but not to an onset-target. Based on this data, they proposed the “contingent capture” hypothesis, which postulates that only those stimuli that are contingent with the attentional set of the observer

will capture attention. In other words, this hypothesis predicts that when looking for something red, only red objects would capture our attention. However, as it will be discussed in the next section, the evidence supporting this idea is mixed, and is currently under debate [44–46].

A different line of research has shown that task set can modulate exogenous cuing effects, both facilitation and IOR. Lupiáñez and colleagues [47–50] have consistently demonstrated that facilitation is larger in magnitude in discrimination tasks as compared with detection tasks, while IOR is larger, and appears sooner, in detection tasks than in discrimination tasks. It has been proposed that the more difficult the task at hand, the greater the orienting of attention produced by the cue [30] and/or the longer attention would remain oriented to the cued location [50]. Klein [30] proposed that because discrimination tasks are more difficult than detection tasks, attention is captured to a greater degree by the cue, giving rise to larger facilitatory effects, and a later disengagement of attention, which delays the appearance of IOR. This hypothesis has recently been challenged by using a paradigm in which participants had to locate or discriminate both target and cue features. Contrary to Klein's proposal, it was demonstrated that a deeper processing of either the cue or the target actually anticipated, rather than delayed, the onset of IOR [51]. Moreover, Lupiáñez and colleagues have recently demonstrated that orienting attention to, or disengaging attention from, the cued location cannot fully explain the task differences in exogenous cuing effects [52]. In their experiments, target type (and the task to be performed with it) was manipulated within a block of trials, which ensured that participants could not know in advance which target would be presented, and thus, the processing of the cue would be equal for all targets. Moreover, their results showed that cuing effects depended on the type of target, with IOR being observed for frequent (to-be-detected) targets, and facilitation being observed for infrequent (to-be-discriminated) targets. This pattern of data cannot be explained by the engagement or disengagement of attention before the target was presented, as the same orienting of attention presumably took place, given that participants could not know the identity of the target in advance. The data

were accounted for in terms of post-orienting processing, concerning the interaction between the processing of the cue and the target.

Klein [53] also explored whether target frequency interacted with endogenous and exogenous attention. He found that exogenous facilitation was similar for frequent and infrequent targets, although endogenous attentional effects were only significant for frequent stimuli. Thus, target frequency affected endogenous but not exogenous orienting of spatial attention. However, more recently, Ivanoff and Klein [54] explored whether target frequency interacted with another exogenous attentional effect, namely IOR. They found that IOR interacted with target frequency in the same way as endogenous attention does (i.e. IOR was larger for frequent than infrequent targets). These results led Ivanoff and Klein to wonder whether IOR might have a component related to endogenous orienting. They also suggest that IOR could be different in nature from exogenous facilitation, in spite of both being considered as an exogenous attentional effect.

In summary, the results reviewed in this section suggest that exogenous orienting of attention is not completely automatic, because it can be modulated by both endogenous spatial attention and task demands (see [41]; for a review). This evidence can be interpreted as indicating that endogenous and exogenous attention consist of the same attentional system that can be oriented in two modes. However, in the next section we will review other studies that have shown effects of exogenous attention independently of endogenous orienting of spatial attention.

### 2.3. Exogenous orienting independently of endogenous orienting

In contrast to the above described “contingent attentional capture” hypothesis, it has been argued that the exogenous capture of attention is a purely stimulus-driven phenomenon that cannot be modulated by endogenous attention [55,56]. Unlike Folk et al. [42,43], Theeuwes and co-workers have proposed that exogenous attention is purely automatic and does not depend on the task set of the observer. They postulated that exogenous attention is always captured by the most salient stimulus. However, if this stimulus turns out not to be a relevant target for the task at hand, attention could be quickly “disengaged”. In order to test for this hypothesis, Theeuwes et al. [45] varied the time interval between the onset of the distractor and the onset of the target, and found that the distractor only produced a cost when it was presented either 50 or 100 ms before target onset; no cost was observed when the distractor was presented 150 ms before target onset. This indicates that attention had been captured early on and “recovered” by 150 ms (see [57], for similar results).

Folk and Remington [44] also tried to test the “recovery account” by using a modified version of the cuing paradigm in which a colored distractor, which could match or not the color of the target (i.e., the participants’ attentional set) preceded the target. The critical manipulation, however, was the appearance of a gray, response compatible/incompatible character simultaneous with the distractor, and at the distractor location. That is, the distractor’s associated response could be either similar to the target’s response (compatible) or different to the target’s response (incompatible). The rationale of this manipulation was that if the distractor did not capture attention when its color did not match that of the target, the identity of the character should not affect target discrimination. The results revealed that responses to the target were faster when a compatible character was presented at the same location as the target, suggesting that the distractor captured attention. More importantly, this effect was significant both when the color of the distractor matched that of the target and when it did not, although the size of the effect was smaller when the colors did not match (see [58]; for further evidence against the later disengagement hypothesis). This further suggests that exogenous attention can take place

in the absence of a contingent task set, although it can be modulated by task set (an endogenous factor). Yantis [59] has recently proposed that salient items “win” the competition in primary visual areas, and once they do, this signal propagates to other levels of the visual hierarchy, increasing the likelihood that the stimulus enters visual awareness. Thus, exogenous effects are combined with, and modulated by, endogenous effects to determine the overall attentive state of the brain.

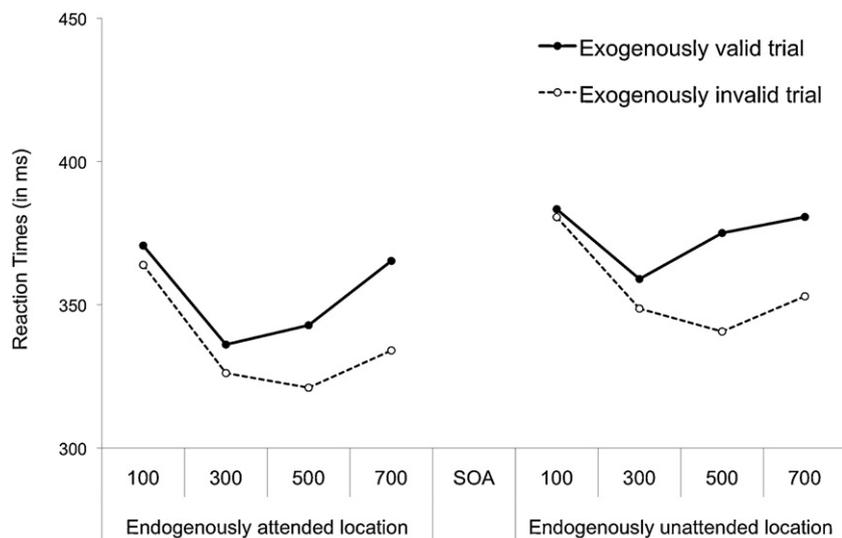
Further evidence about the independence of endogenous and exogenous attention comes from studies demonstrating that cuing effects (facilitation and IOR) can be independent of endogenous orienting [47,60–65]. In all these studies, which used different experimental paradigms, similar facilitation and IOR effects have been shown at endogenously attended or unattended locations, i.e. endogenous spatial orienting did not modulate exogenous orienting effects (see Fig. 2). Lupiáñez et al. [64] reanalyzed the results of a previous study by Bartolomeo et al. [66], exploring the performance of patients with right brain damage and left unilateral neglect. These patients showed a lack of IOR for right, ipsilesional targets ([67,68]; see also [69]), which is consistent with the idea that these patients’ attention is biased towards right, ipsilesional objects [70]. Lupiáñez et al.’s [64] reanalysis of Bartolomeo et al.’s results demonstrated that the lack of IOR was present for both endogenously expected and unexpected right-sided targets, indicating that endogenous and exogenous attention (IOR) can produce their effects independently, without interacting with each other.

### 3. Endogenous and exogenous orienting mechanisms independently contributing to performance

Rather than exploring quantitative differences, a different approach to study whether endogenous and exogenous attention constitute two different attentional systems is to explore their qualitatively different effects on information processing. In particular, finding a double dissociation on the effects of endogenous and exogenous attention would support the idea that both systems can work independently of each other. The following table (modified with permission from [21]) shows a summary of all the differential effects of endogenous and exogenous attention on the processing of information that we know of so far.

Some of the data presented in Table 1 can easily be explained by a single system orienting attention either endogenously or exogenously. Endogenous orienting is slower and more susceptible to interruption than exogenous orienting [34]. Endogenous attention is affected by cue predictivity [34], and does not produce IOR. In fact, it has been proposed that endogenous attention to the location of a peripheral cue would mask the appearance of IOR [32]. Considering attention as a single mechanism (which may be oriented in two modes, endogenously or exogenously), Posner et al. [27] postulated that IOR was an attentional mechanism caused by the inhibition of the return of attention to a previously attended position. According to this hypothesis, when a peripheral cue appears, attention is automatically drawn to its position, but because the cue is not predictive of the target location, attention is disengaged from that spatial position, and an inhibitory mechanism starts to operate, inhibiting the return of attention to that previously attended position. This hypothesis would predict that IOR would not be observed until attention is disengaged from the cued location. However, as already mentioned, it has been consistently demonstrated that IOR can be dissociated from endogenous orienting, being observed at endogenously attended locations, from where no disengagement of attention has taken place [47,61–64] (see Fig. 2).

In fact, most of the data presented in Table 1 are more easily explained by assuming the independence of the two systems. Particularly, exogenous attention to a part of an object spreads to the whole object automatically, although endogenous



**Fig. 2.** Results from Chica et al. [47], Experiment 2: Mean RTs to detect targets presented at different SOAs, in exogenously valid and invalid locations that could either be endogenously attended or unattended. In this paradigm peripheral cues were used. In one block of trials, the cue predicted the target to appear at the same spatial location with high probability. In the other block, the cue was counterpredictive, indicating target appearance at the opposite location with high probability. Exogenously valid and invalid trials refer to conditions in which the target was presented at the same location than the cue (valid) or at a different location (invalid). Endogenously attended trials refer to those trials in which the target appeared at the location predicted by the cue (the cued location for predictive cues, and the uncued location for counterpredictive cues), while endogenously unattended trials refer to those trials in which the target appeared at the non-predicted location (the uncued location for predictive cues, and the cued location for counterpredictive cues). The results demonstrate that IOR (slower RTs for exogenously valid vs. invalid trials) was identical at endogenously attended and unattended location, suggesting that (1) IOR (an exogenous attentional effect) is independent of endogenous orienting; (2) IOR is observed at endogenously attended locations, from where no disengagement of attention has taken place.

**Table 1**  
Dissociations between endogenous and exogenous attention.

Behavior	Endogenous	Exogenous
Speed (1)	Slow	Fast
Disruption by memory load (1)	Yes	No
Cue predictability (1)	Yes	No
Spread on objects (2)	Not necessarily	Yes
Meridian Crossing effect (3)	Yes	Facilitation: No IOR: Yes
Disengage deficit after parietal injury (4)	No	Yes
Inhibition of Return (5)	No	Yes
Stimulus enhancement (6)	No	Yes
Interaction with visual search tasks (7)	No	Yes
Interaction with non-spatial expectancies (7)	Yes	Facilitation: No IOR: Yes
Modulation of Spatial Stroop (8)	Increase	Decrease
Effects on early perceptual processes (9)	Smaller	Larger
Effects on later decisional stages (9)	Yes	Facilitation: No IOR: Yes
Produces Illusory Line Motion (10)	No	Yes
Modulates conscious perception (11)	No (or weakly)	Yes

(1) Jonides [34] and Müller and Rabbitt [29]. (2) Egly et al. [86] and Macquistan [185], but see Abrams and Law [186], and Goldsmith and Yeari [71]. (3) Reuter-Lorenz and Fendrich [72]; Tassinari et al. [73]. (4) Bartolomeo and Chokron [70], see also Losier and Klein [187] for a review. (5) Posner and Cohen [26]. (6) Lu and Doshier [188], but see Prinzmetal et al. [78]. (7) For a review see Klein and Shore [80]; see also Ivanoff and Klein [54]. (8) Funes et al. [84]. (9) Chica and Lupiáñez [63], see also Hopfinger and West [77]. (10) Christie and Klein [74] and Chica et al. [75]. (11) Chica and Bartolomeo [7] for a review.

attention only spreads to objects when specific instructions are given or when the attentional focus is controlled to be broad [71]. The possibility that exogenous attention is more object-based than endogenous attention is can also explain the differences concerning the meridian crossing effect. In these experimental paradigms, stimuli locations are manipulated so that the objects can appear on

either the same location of a vertical meridian or on different meridians. The effect consists of slower RTs when the cue and target are presented on opposite sides of the vertical meridian as compared to the same side, once distance is equated. The meridian effect is only observed with endogenous cues, but not with exogenous cues leading to facilitatory effects [72]. We reckon that if exogenous attention were object-based, the hemisphere in which the cue and target are presented would not have any effect. However, if endogenous attention were more space-based, then a meridian effect is expected to occur. Paradigms measuring IOR have reported that, as endogenous orienting, IOR shows the meridian crossing effect [73], suggesting that IOR can behave like endogenous orienting, rather than like facilitatory exogenous orienting effects (see also [54], described above).

The modulation of endogenous and exogenous attention on the “Illusory Line Motion” effect (ILM) could also be interpreted within this object/space-based framework. ILM consists of an illusory perception of motion away from a cue when a line is presented all at once near a previously cued or stimulated location. ILM is observed when attention is attracted exogenously to one of the edges of a line (by presenting a peripheral cue). Endogenous attention only produces the effect when attention is object-based, but not space-based [74]. Moreover, endogenous attention does not produce the ILM effect by itself, although maintaining endogenous attention at the location of a peripheral cue increases the ILM effect when the task set favors the integration between the cue and the line [75].

Exogenous and endogenous forms of attention also differ in the stages of processing at which they produce their effects. Exogenous attention has been shown to produce signal enhancement and external noise reduction, while endogenous attention only affects external noise reduction [76]. By using event-related potentials (ERPs), it has been demonstrated that at short Stimulus Onset Asynchronies (SOAs), exogenous attention (facilitatory effects) produced stronger effects on perceptual components (such as P100) than endogenous attention does [77]. At longer SOAs, IOR affected both early and late stages of processing as measured by P100 and P300 modulations, respectively [63], while endogenous attention

produced stronger effects at late stages of processing (P300). This evidence contrasts with the conclusions reached by Prinzmetal et al. [78], who claimed that endogenous attention produce signal enhancement, while exogenous attention affects the decision of where to respond. However, in Prinzmetal et al.'s experiments, exogenous attention is manipulated by using a non-predictive peripheral cue, while endogenous attention is always manipulated by making the peripheral cue predictive of the target's location. Given that informative peripheral cues attract both exogenous and endogenous attention to their location, it is not clear whether the results reported by Prinzmetal et al. [78] in RT and accuracy experiments are pure dissociations between the effects of endogenous and exogenous attention, or whether endogenous attention elicited by peripheral cues can enhance the effects of exogenous attention or produce further interactions between the exogenous and the endogenous attentional systems [47,79].

Another issue of interest concerns the possibility of differential influences of endogenous and exogenous spatial attention on conscious visual perception. Recent behavioral studies have demonstrated that while endogenous attention produces a weak influence on the conscious perception of near-threshold targets (see also [12,14]), exogenous attention is an important modulator of conscious perception [9]. In different experiments, Chica et al. [9,181] triggered spatial attention by using either peripheral or central symbolic cues (such as letters or colors indicating the location of the upcoming targets). In the case of peripheral cues, they were non-predictive, predictive, or counter-predictive of where the target would appear. Therefore, participants could have no incentive to orient endogenous attention to the cued location, had an incentive to maintain attention at the cued location, or to remove attention from the cued location, respectively. The results demonstrated that the key factor modulating conscious perception was how spatial attention was triggered, rather than how it was maintained. Exogenously triggered attention using peripheral cues increased the proportion of seen targets at the cued location. Moreover, in order to produce modulations in perceptual sensitivity (and not only in response criterion) endogenous attention needed to be maintained at the cued location (i.e., this modulations were only observed in the case of predictive peripheral cues). These results indicate that rather than how spatial attention is maintained, modulations depended on how spatial attention is triggered. Endogenous attention to the location of a peripheral cue can enhance the exogenous effects produced by peripheral cues, which is a clear case of interaction between endogenous and exogenous attention.

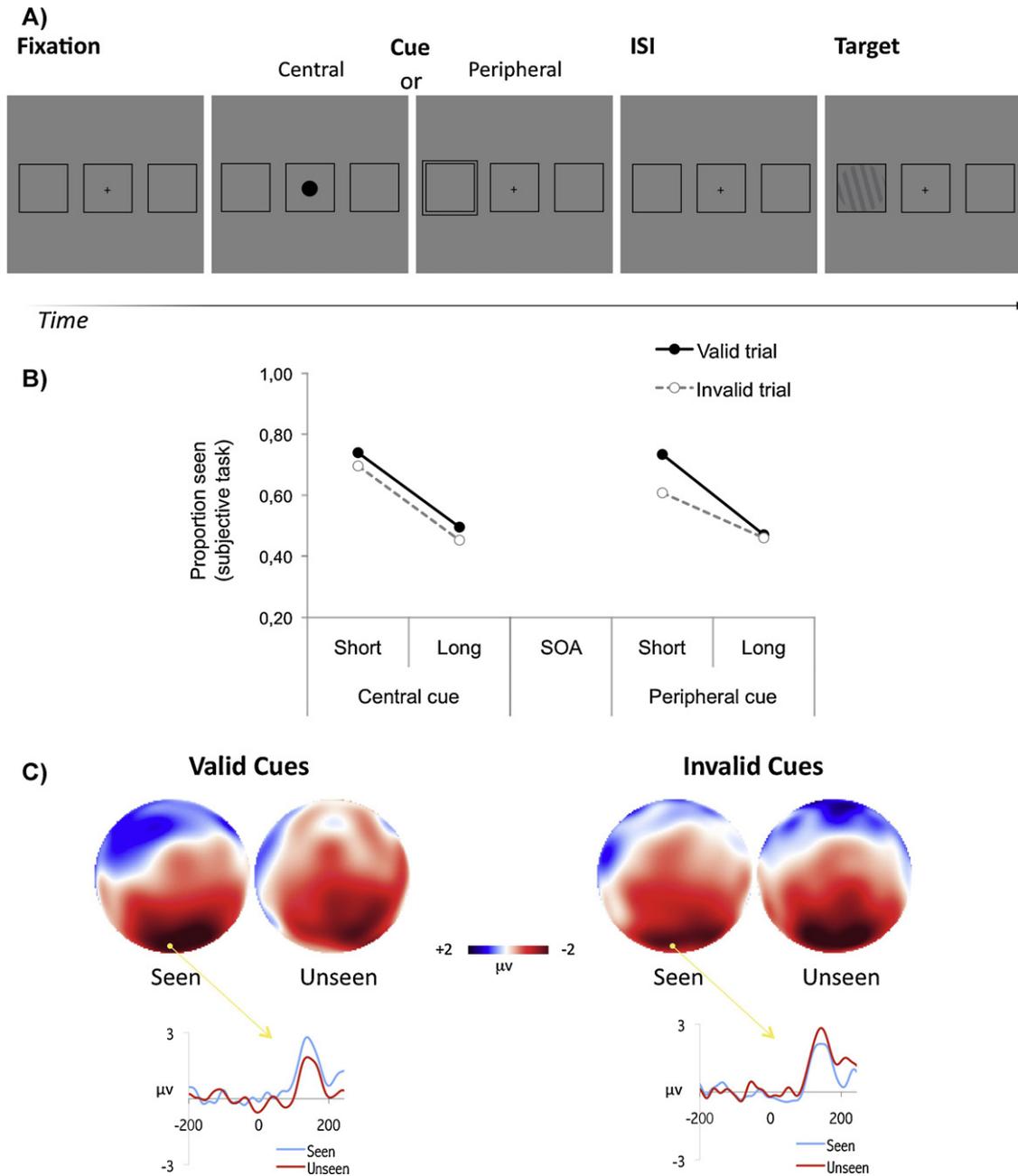
Consistent with this behavioral evidence, several studies have demonstrated that while endogenous attention can be electrophysiologically dissociated from conscious perception, exogenous attention cannot [8]. By using magneto-encephalography, Wyart and Tallon-Baudry [14] demonstrated that whether attended or not, consciously perceived stimuli modulated mid-frequency gamma-band activity over the contralateral visual cortex, whereas spatial attention modulated high-frequency gamma-band activity, independent of whether targets were consciously perceived or not. However, when spatial attention was oriented exogenously, cue-related ERP components have been strictly linked to subsequent conscious reports. For example, in Chica et al. [10], a cue-related P100 component was larger for subsequently seen targets than for unseen targets when attentional cues were valid; in contrast, P100 was larger for subsequently unseen than for seen targets when attentional cues were invalid. The P100 component elicited by the cue might well index the capture of attention that the cue produced. Thus, if valid cues captured attention to the location of the impending target, then more targets would be consciously perceived at that location. However, if an invalid cue captured attention to a wrong location, fewer targets would be consciously perceived. It was

suggested that exogenous attention gates information processing to facilitate access to consciousness, while endogenous attention might be necessary to maintain the processes triggered by the peripheral cue, allowing for the reverberating flow of information that is needed to achieve conscious perception [7] (see Fig. 3).

From all this evidence of differential effects produced by endogenous and exogenous attention, two dissociations deserve special attention. The first dissociation, reported by Klein and Shore [80], concerns the effects of endogenous and exogenous attention in feature and conjunction search tasks. Briand and Klein [81,82] observed that the effect of exogenous attention and task (feature vs. conjunction search) interacted, while the effect of endogenous attention was additive to task. Although the interacting effect of task with exogenous attention has been shown to depend on cue-target predictivity [83], the critical feature is that it only occurred with peripheral cues. On the other hand, Klein [53] observed that when non-spatial expectancies such as target frequency were manipulated, the manipulation affected endogenous attention, but not exogenous attention. When these two pieces of data are taken together, they constitute a double dissociation between exogenous and endogenous attention, which strongly support the independence of the two attentional systems. Klein and Shore [80] concluded that exogenous attention affected early perceptual processes related with feature binding while endogenous attention affected later decisional processes.

But perhaps the clearest evidence for functionally dissociable attentional orienting systems was observed by Funes et al. [84], who reported the first double dissociation,<sup>1</sup> within the same experiment, between the qualitative effects of endogenous and exogenous attention. They studied the effects of endogenous attention (by using spatially informative purely symbolic color central cues), and exogenous attention (by using peripheral cues), in a spatial Stroop task. In this task, an arrow is presented either to the left or to the right of the fixation point. The arrow can also be pointing either left or right, and participants are required to respond to the location the arrow is pointing at. Note that when the arrow is presented on the left pointing left, the location where the arrow is presented is congruent with the location the arrow is pointing at. However, when the arrow is presented on the left pointing right, the location of the arrow is incongruent with the location the arrow is pointing at. Generally, RTs are faster on congruent than incongruent trials (i.e., the spatial Stroop effect). Interestingly, Funes et al. showed that the spatial Stroop effect was differentially modulated by endogenous and exogenous attention: while exogenous attention decreased the spatial Stroop effect (smaller effect at the cued location, mostly at short SOAs), endogenous attention increased the spatial Stroop effect (larger effect at the endogenously attended location, mostly at longer SOAs) (see Fig. 4). In line with the object- versus space-based characteristics of endogenous and exogenous attention discussed above, it has been demonstrated that the reduction of the spatial Stroop effect induced by peripheral cues is object-based, not space-based [85]. The

<sup>1</sup> Hein et al. [189] have also reported a dissociation on the effects of endogenous and exogenous attention on temporal resolution tasks. Yeshurun and Levy [190] were the first to observe that exogenous attention impaired temporal resolution tasks such as detecting a gap within two sequentially presented stimuli. Hein et al. [189] extended this finding by reporting that while exogenous attention (triggered by either non-informative or informative peripheral cues) impaired temporal resolution tasks, endogenous attention (triggered by a central informative cue) enhanced performance on those tasks. However, Chica and Christie [191] controlled for speed-accuracy trade-offs using an exogenous cuing paradigm, and found that when response time was constricted, exogenous attention enhanced, rather than impaired, performance in temporal resolution tasks. Therefore, both endogenous and exogenous attention can enhance temporal resolution, although exogenous cuing paradigms (using peripheral cues) are likely to produce speed-accuracy trade-offs in these kinds of tasks.



**Fig. 3.** (A) Graphical illustration of a paradigm used to manipulate spatial attention and conscious perception using central and peripheral cues [9]. The central cue dot was colored in green or red, indicating with high probability the location of target appearance. The peripheral cue was presented near the right or left marker, and could be predictive or non-predictive of target location. (B) Proportion of consciously detected targets presented at valid and invalid locations when central and peripheral predictive cues preceded near-threshold targets at short and long SOAs (results from [9], Experiment 5). The results show that unlike central cues, peripheral cues increased the proportion of consciously detected targets at the attended (valid) vs. the unattended (invalid) location, mostly at short SOAs. (C) Topographic distribution of the P100 effect, 120 ms after cue appearance; and event-related cue-locked potential waveforms for valid and invalid peripheral cues, leading to seen and unseen reports (adapted from [10]). The figure shows that for valid cues, P100 is larger for subsequently seen than unseen targets; for invalid cues, P100 is instead larger for subsequently unseen than seen targets.

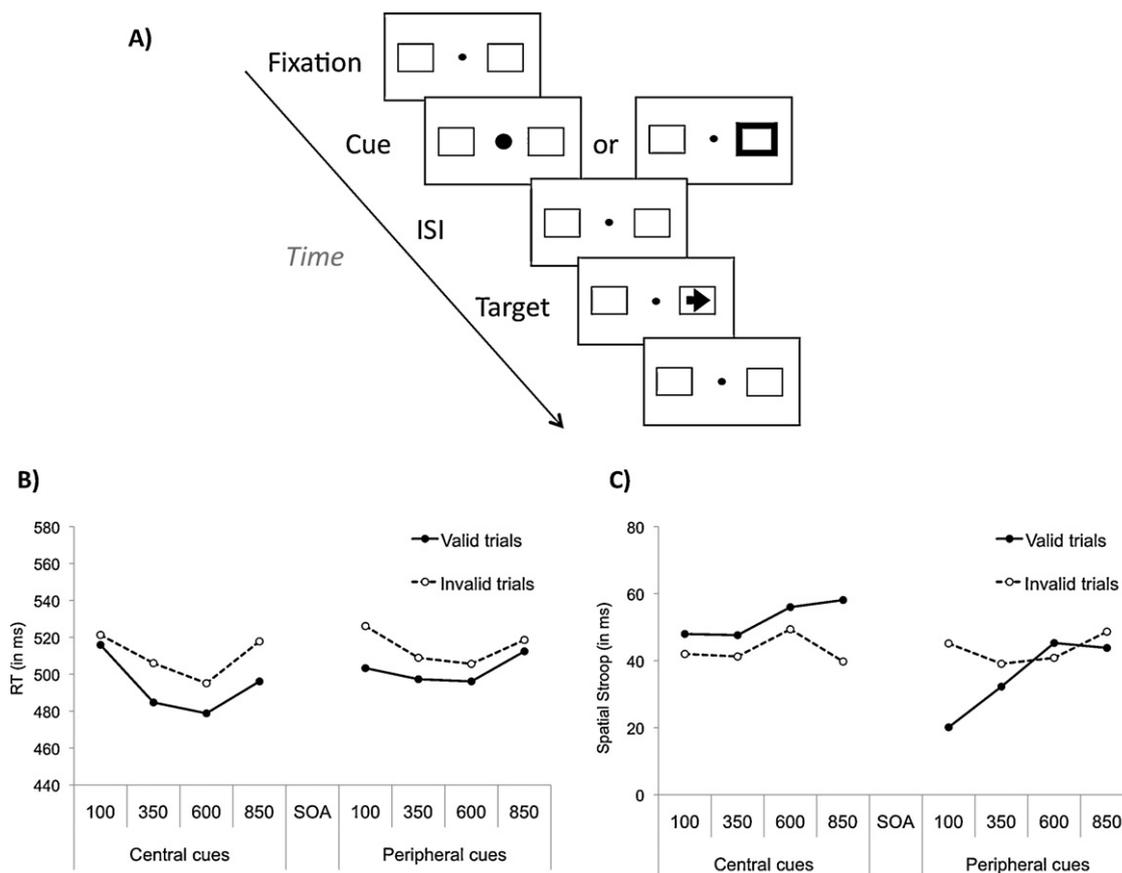
reduction of the spatial Stroop does not only occur at the location of the peripheral cue, but it spreads to the entire object where the cue has been presented [86].

In summary, the results presented in this section indicate that endogenous and exogenous attention are two functionally distinguishable attentional systems, with different effects on information processing. While exogenous attention produces an effect on early perceptual stages, modulating feature binding and perceptual integration, endogenous attention influences later stages of processing, probably affecting the decision of where to respond. If endogenous

and exogenous attention constitute two different attentional systems, they should also be implemented in at least partially distinct neural circuits. In the next section we will review neuropsychological and neuro-imaging evidence on the dissociation between endogenous and exogenous attention.

#### 4. Neural systems of endogenous and exogenous attention

Before reviewing the studies that have attempted to dissociate the neural basis of endogenous and exogenous orienting, we



**Fig. 4.** (A) Schematic view of the Spatial Stroop task, in which either central predictive cues or peripheral non-predictive cues preceded the targets [84]. The central cue dot was colored in green or red, indicating with high probability the location of target appearance. (B) Mean RTs for valid and invalid conditions as a function of SOA, for central predictive cues and peripheral non-predictive cues (results from [84], Experiment 1). Results demonstrate that participants were paying attention to the location indicated by the central cue, mostly at the longest SOA; and to the location signaled by the peripheral, mostly at the short SOA. (C) Spatial Stroop effect (incongruent minus congruent trials) as a function of validity and SOA, for central predictive cues and peripheral non-predictive cues (results from [84], Experiment 1). Results demonstrate that the Stroop effect is increased for valid vs. invalid trials when central cues attract attention, mostly at the longest SOA, where larger validity effects were observed in RT. Interestingly, the Stroop effect is decreased for valid vs. invalid trials when peripheral cues attract attention, mostly at the shortest SOA, where larger validity effects were observed in RT.

will consider previous literature investigating the brain networks associated to (mostly endogenous) orienting and reorienting of attention to unexpected events. The effects of core attentional regions on visual cortical areas will then be described. Finally, we will present the state of the art concerning the research on the neural systems underlying endogenous and exogenous orienting.

#### 4.1. Dorsal and ventral fronto-parietal networks for the control of orienting

During the last decades, numerous neuro-imaging studies have demonstrated that spatial orienting is implemented in a bilateral network with core regions in parietal and frontal brain areas [87–98]. Hopfinger et al. [90] presented one of the first functional Resonance Magnetic Imaging (fMRI) studies to dissociate activity related to cue processing from target-related activity (i.e. brain activity associated to the attentional orienting period and to the target identification period). This study provided important clues about the function of each region for attentional orienting. A network of cortical areas including superior frontal, inferior parietal, and superior temporal brain regions were implicated in endogenous attentional control, as they were found to be active only in response to the cues. In contrast, other regions of the cortex, including the ventrolateral prefrontal cortex, the anterior cingulate, and the supplementary motor area were found to be selectively activated by target stimuli, suggesting that these areas were more

involved in selective stimulus processing and/or in response mechanisms. Activation in the intraparietal sulcus (IPS) in response to the cues, but not to the targets, suggested that the inferior parietal lobule is involved in attentional orienting processes. Other findings support a role for IPS in the endogenous orienting and maintenance of attention to a target location. First, the presentation of a central cue indicating the most likely location of a subsequent visual target triggers transient responses in the occipital cortex, but more sustained responses in IPS. Second, when the delay after cue offset is extended for several seconds, forcing participants to maintain attention at the cued location for longer periods, IPS is the only brain region that showed a sustained response during the delay [99].

Medial regions of the prefrontal cortex (including the Supplementary Eye Field, SEF) and the superior parietal lobe (SPL) generate transient activity for disengaging attention from fixation and moving it to a new location ([100]; see also [98]). Regions of the SPL are engaged in shifts of attention between locations, features, objects, and sensory modalities [98,101–103]. By contrast, activity in the Frontal Eye Field (FEF) and the IPS represents sustained maintenance of attention at peripheral locations [100]. Thus, the SPL would track the locus of spatial attention by encoding changes in spatial coordinates [104], whereas IPS and FEF would index the current locus of attention in the visual field.

A region of the right hemisphere at the intersection between the parietal and the temporal cortex, the temporo-parietal junction (TPJ) has consistently been shown to be engaged during target

detection [99]. Unlike other parietal regions that show both cue and target-related responses (such as the anterior and ventral IPS), the right TPJ shows little if any response to the cue. It is strongly engaged when targets are presented at unattended vs. attended locations. Moreover, coupling between visual occipital areas and the right TPJ selectively increases during unattended location trials, when reorienting is required [105]. There is a clear lateralization of the effect, because these TPJ responses are much stronger in the right hemisphere than in the left hemisphere. However, recent data have demonstrated that left TPJ is also activated when responses to valid trials are compared to neutral (rather than to invalid) trials [106].

The right lateralization of TPJ responses is consistent with deficits observed in the neglect syndrome after lesions of the right parietal cortex or of its connections to the ipsilateral frontal lobe [68,107]. Several studies have demonstrated that although dorsal regions (including FEF and posterior parts of the SPL) respond to stimuli presented on either side, their response to contralateral stimuli is larger than that to ipsilateral ones [108]. The most obvious asymmetry on the system is observed in the right supramarginal gyrus (SMG, part of TPJ region), which responds equally to left and right stimuli, while the left SMG seems not to respond at all [108]. Based on these data, it has been proposed that the right TPJ/SMG may not carry a topographic representation of the visual space, because it is not influenced by the location of the stimulus. It might instead be involved in alerting when a potentially relevant stimulus appears [108], or in re-orienting to unexpected but task-relevant events ([99]; see below). Szczepanski et al. [109] also reported a strong spatial bias toward the contralateral visual field in multiple higher-order topographic areas. The extent of activations in the right hemisphere tended to be larger than in the left hemisphere [87,89,93], and many voxels showed a preference for the contralateral visual space [110–113]. Importantly, two hemispheric asymmetries were noted. Only the right SPL, but not the left SPL, carried attention signals, whereas the left FEF and the left IPS generated stronger contralateral attention signals than their right-hemisphere counterparts. The left FEF and IPS may counteract the right hemispheric asymmetry and balance the frontoparietal system for spatial attentional control. Additionally, the IPS seems to play an important role in the coding of visual saliency maps. Studies in monkeys [114,115] and humans (see [116]; for a review; [117]) have demonstrated that the intraparietal area contains an explicit two-dimensional map that encodes the saliency or conspicuity of objects. This map may subservise a wide range of behaviors including, but not limited to, saccadic eye movements, required for coherent visual exploration and for the control of visually guided behavior.

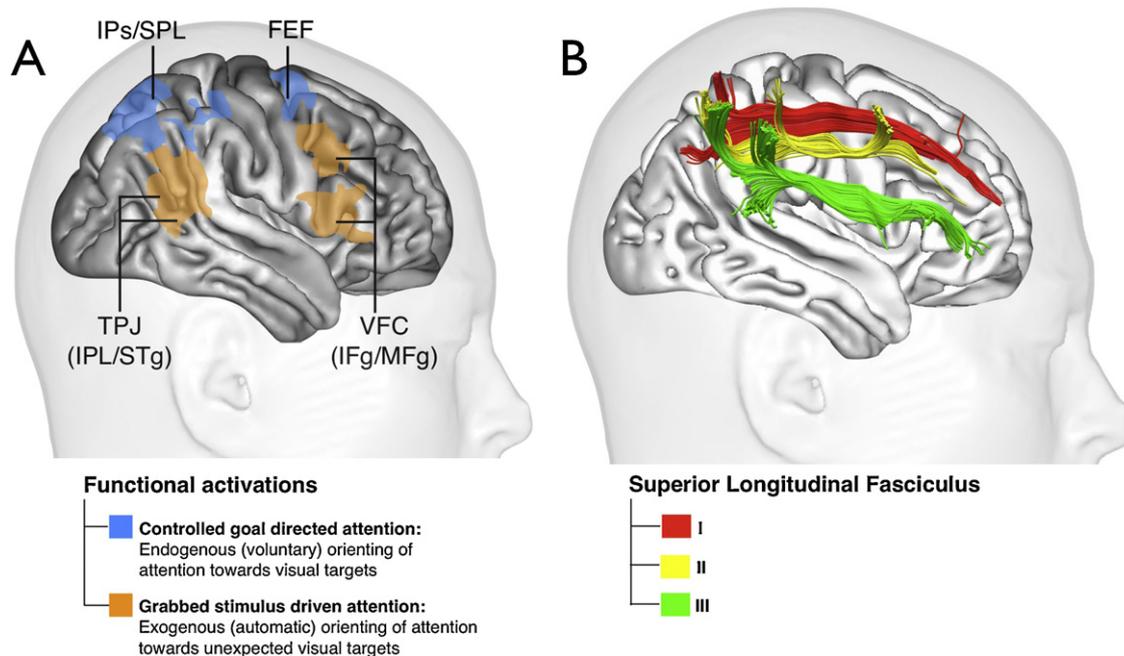
A recent model has been proposed, in which dorsal and ventral fronto-parietal regions are segregated into two anatomical and functional networks [99,118] (see Fig. 5). The dorsal fronto-parietal network enables the selection of sensory stimuli based on internal goals or expectations (goal-driven attention) and links them to appropriate motor responses. A ventral fronto-parietal network detects salient and behaviorally relevant stimuli in the environment, especially when unattended (stimulus-driven attention). The dorsal fronto-parietal network, whose core regions include the dorsal parietal cortex, particularly the IPS and SPL, and the dorsal frontal cortex along the precentral sulcus, near or at the FEF, has been associated to endogenous control mechanisms [119,120]. The dorsal network is pre-activated by the expectation of seeing an object at a particular location or with certain features, by the preparation of a specific response, or by the short-term memory of a visual scene (see [118]; for a review). The dorsal system is also involved in linking relevant stimuli to responses, as it is modulated when people change their motor plan for an object [121]. Under some conditions, the preparatory activation of the dorsal

frontoparietal network extends to the visual cortex, presumably reflecting the top-down modulation of sensory representations (see below).

The right TPJ would be part of a second system, the ventral attentional network. This system is not activated by expectations or task preparation but responds along with the dorsal network when behaviorally relevant objects (or targets) are detected [122]. Both dorsal and ventral networks are also activated during reorienting, with enhanced responses during the detection of targets that appear at unattended locations. Core regions of the ventral network include the TPJ and the ventral frontal cortex (VFC), including parts of the middle frontal gyrus (MFG), the inferior frontal gyrus (IFG), the frontal operculum, and the anterior insula. Different nodes of the ventral fronto-parietal network respond to reorienting and expectation of reorienting. While the right TPJ is activated anytime reorienting is necessary independently of expectation, the right IFG is activated by stimulus-driven reorienting but only when reorienting is unexpected [106,123]. This ventral fronto-parietal network is activated by task-relevant events presented at unattended locations, even when these events have a low perceptual salience. Conversely, the presentation of high-salience stimuli in one hemifield while endogenous attention is engaged elsewhere does not activate the ventral network [124]. Task-irrelevant stimuli that share features with task-relevant targets compete for attention and modulate the TPJ and IFG [112,125]. The ventral attention network is distinguished under resting conditions from a second network, comprising the bilateral dorsal basal ganglia, the anterior cingulate, the left dorsolateral prefrontal cortex (DLPFC), and the left anterior insula, which is also recruited by stimulus-driven shifts of attention, but only to unexpected stimuli. The role of this network has been less explored, and it has been proposed that it may retrieve/activate commands for shifting attention [123].

The right TPJ has been found to deactivate in response to irrelevant distractors [126], with larger deactivation when subsequent targets were detected than when they were missed [127]. Furthermore, the set of potentially interfering stimuli filtered out by the right TPJ [127] was found to substantially vary according to the presence of a behavioral context [128] and its demands. Todd et al. [129] reported that increases in visual short-term memory load are correlated with greater mean deactivations in the right SMG, suggesting that increased visual short-term memory load suppressed right SMG activity in order to prevent orienting to irrelevant stimuli. During spatial orienting, the right TPJ deactivates when cue validity increases. The higher the cue validity, the greater the right TPJ deactivation, and the filtering out of the unattended location. Reduced filtering of the unattended location with low validity cues was associated with a drop in attentional costs without affecting attentional benefits ([106]; see also [130]).

For the attentional system to act in a coherent way, there need to be interactions between the ventral and the dorsal frontoparietal networks. Regions within the lateral prefrontal component of the ventral attention network are proposed to be a site of convergence for dorsal and ventral frontoparietal networks. Asplund et al. [131] suggested that the right inferior frontal junction (IFJ; located in the posterior aspect of the inferior frontal sulcus, parts of Brodmann areas 9, 44, 6) might not only be a core member of the ventral attention network that supports stimulus-driven attention, but it would also be functionally integrated with the dorsal attentional network during goal-directed behavior. The IFJ supports goal-directed behavior, as it is activated along with core members of the dorsal network during the cue period of a classic goal-directed attention task. Connectivity analyses showed that IFJ activity was correlated positively with activity in the FEF and IPS, but negatively with TPJ activity. Conversely, when reorienting was necessary, IFJ–FEF and IFJ–IPS correlations decreased, whereas those between the IFJ and TPJ increased, and those between the FEF and IPS did not change.



**Fig. 5.** (A) Right-hemisphere networks of visuospatial attention according to Corbetta and Shulman [99]. (B) The three branches of the Superior Longitudinal Fasciculus according to Thiebaut de Schotten et al. (modified with permission from [140]). The figure represents the anatomical brain regions associated to spatial attention and the white matter branches that might connect them.

This finding is consistent with recent resting state functional connectivity data suggesting that the IFJ functionally interacts with both ventral and dorsal brain structures [132]. Resting-state analyses also suggest that part of the ventrolateral frontal cortex, the right MFG, may link dorsal and ventral networks [133].

Spatial biases in patients with left neglect have also been shown to depend on a physiological imbalance between the left and right dorsal parietal cortex (IPS/SPL), which is caused by structural and physiological abnormalities in the ventral attention network [132,134]. The inter-hemispheric imbalance in the IPS/SPL is evident both during spatial attention tasks, with a significant relationship between left-side neglect and relative hyperactivation of the left parietal cortex, and in measures of functional connectivity at rest. Interestingly, the degree of functional impairment in the dorsal parietal cortex correlates with the degree of impaired functional connectivity in the structurally damaged ventral network, hence demonstrating the interaction between the two networks. Notably, this interaction involves the right MFG, and the white matter fibers connecting this region to the dorsal parietal cortex [132], providing more support for the hypothesis that the right MFG links ventral and dorsal systems.

In recent years, there has been a renewed interest in the anatomical connections between cortical and subcortical gray matter regions (the so-called hodotopic approach; [135]), thanks to advances in neuroimaging techniques such as Diffusion Tensor Imaging tractography [136]. These studies are particularly important as they demonstrate how brain regions are interconnected and therefore suggest their possible functional relations. The topological approach (based on the study of isolated brain regions) has proved to be very successful in exploring which brain regions support each cognitive function. However, the communication within brain regions is essential to understand how different brain systems interact, and how cognitive functions may emerge from these interactions. Brain damage resulting in attentional problems, such as those demonstrated by patients with spatial neglect has been correlated with dysfunction in large-scale cortical networks

[107,137,138]. Studies on both animal models and human patients have recently stressed the importance of long-range white matter pathways in normal attention and its deficits [139–142] (see Fig. 5). The superior longitudinal fascicle (SLF), as well as the arcuate fascicle (AF), and the inferior fronto-occipital fascicle (IFOF) are thought to provide connectivity for spatial attention [107,132,138]. Recent data in the human brain [140] have revealed a dorsal to ventral gradient of lateralization of the SLF. While its most dorsal branch, the SLF I, is symmetrically distributed between the left and the right hemisphere, an intermediate branch, the SLF II, shows a trend for right lateralization; the most ventral branch, SLF III, is instead right-lateralized. Importantly, the anatomical asymmetry of the parieto-frontal connections predicted asymmetries of behavioral performance on visuospatial attention tasks in normal participants. Moreover, the cortical projections of the SLF I overlap with the dorsal attentional network activated during orienting of spatial attention, and the SLF III overlaps with the ventral attentional network that is activated during stimulus-driven reorienting. In contrast, the SLF II overlaps with the parietal component of the ventral network and the prefrontal component of the dorsal network. SLF II might therefore represent a direct communication between the dorsal and ventral networks. Signals relayed by the SLF II may act as a modulator for the dorsal network, redirecting goal-directed attention mediated by the SLF I to events identified as salient by the SLF III [140].

#### 4.2. Effects of attentional networks on cortical visual areas

The fronto-parietal brain regions subserving attentional orienting reviewed above are considered as the source of attentional operations, implementing orienting mechanisms. But there are also some other brain regions that constitute the neural expression of attentional processes, which enhance early perceptual processes and motor planning. Neuroimaging studies in humans have revealed topographically targeted attentional modulations in occipital cortex [143–147]. Attention to a particular location in the

visual field activates the retinotopic visual cortex [91], whereas signals representing other locations are suppressed [148,149]. Similarly, when a target is specified by a non-spatial attribute, such as object category (e.g., a face), activity in specialized extrastriate areas (e.g., the fusiform face area) is boosted [102,150,151].

In monkeys performing a visual matching task [152], simultaneous neural recordings from the posterior parietal cortex and an earlier area in the visual pathway (the medial temporal area), demonstrated that when attention was engaged to a particular location, the timing of activities in the two regions became synchronized with the parietal cortex leading the medial temporal area. fMRI studies in humans have also supported the view that the FEF and IPS exert top-down modulatory influences on the visual cortex [99,112,120,149,153,154]. Activity in the FEF and IPS predicts activity in the visual cortex of participants engaged in a visual attention task. The FEF modulates the IPS far more than the IPS modulates the FEF during visual attention [155]. Top-down modulations of intermediate-tier areas (VP, V4) are stronger than those of low-tier areas (V1, V2), which is consistent with the known distribution of attention-related modulations in extrastriate cortex [156–162].

Transcranial Magnetic Stimulation (TMS) studies have also demonstrated the modulation of attentional areas over visual cortical areas (see e.g., [163,164]). Capotosto et al. [165] have recently used repetitive TMS over frontoparietal regions during the allocation of spatial attention to test for interference effects with the subsequent perception of visual stimuli and the desynchronization of alpha rhythms in occipital the cortex. Although TMS did not disrupt the observers' ability to direct spatial attention to the target location, TMS on the right IPS disrupted the desynchronization of anticipatory (pre-stimulus) alpha rhythms in the parieto-occipital cortex. TMS on both the right IPS and the right FEF also disrupted the spatially selective topography of alpha power in the occipital cortex [166–169]. Behavioral deficits in target discrimination correlated, across and within participants, with the degree of alpha synchronization caused by the right FEF and the right IPS interference.

In summary, fronto-parietal areas involved in attentional control modulate the activity of other perceptual regions such as visual regions of the occipital cortex, or occipito-temporal regions in charge of object processing and recognition. Therefore, the source of the attentional system will be implemented in areas of the fronto-parietal network, while the neural effects of attention can be observed in the modulation exerted in perceptual areas of the brain.

#### 4.3. Neural correlates of endogenous and exogenous spatial attention

Some fMRI studies have aimed at comparing the neural correlates of endogenous and exogenous orienting. The first attempts used blocked designs, in which cue- and target-related activity could not be teased apart [87,89,92–95,170]. The results of these pioneering studies led to the conclusion that endogenous and exogenous spatial attention were mediated by the same neural substrate, in apparent contrast with the numerous behavioral dissociations between endogenous and exogenous orienting (see above).

More recent event-related fMRI studies have used a different approach and analyzed the activation related to the cue separately from that related to the target. This approach demonstrated some segregation between dorsal (IPS and FEF) and ventral (TPJ and IFG) fronto-parietal regions, with the former being primarily engaged by the endogenous cues, and the latter activating in response to targets presented at unattended vs. attended locations (stimulus-driven reorienting towards task-relevant stimuli; [99,118]). Nowadays, several authors equate stimulus-driven reorienting and exogenous

attention. However, they refer to conceptually different processes. While exogenous orienting refers to the involuntary capture of attention produced by salient and potentially dangerous stimuli (which can be cues, targets, or even distractors), stimulus-driven reorienting, as observed in the ventral fronto-parietal network, is related to the processing of stimuli that are relevant for the task at hand. Salient but unrelated targets for the current task may capture exogenous attention, although they do not activate the reorienting network.

Several studies have compared the activity of the reorienting system following endogenous and exogenous cues. Natale et al. [171] orthogonally manipulated endogenous and exogenous attention within the same design. They showed that only reorienting signals following endogenous invalid cues modulated activity in the ventral fronto-parietal attentional network. On the other hand, exogenous invalid cues affected activity in the occipito-temporal junction. The pattern of activation associated with each signal was independent from the effect (valid/invalid) of the other cue, which suggested a separation of endogenous and exogenous mechanisms for the reorienting of spatial attention. Hahn et al. [172] employed an attention task that systematically varied the relative contribution of endogenous and stimulus-driven processes to performance. Brain regions involved in the endogenous regulation of visuospatial selective attention were expected to display incremental activation with fewer cued locations (i.e., when attentional selection was better focused in a spatial location). By contrast, stimulus-driven processes should be engaged when attention is drawn to a previously unattended location by the occurrence of a stimulus. As mentioned above, stimulus-driven processes refer to target- but not to cue-related processing. The left IPS, with adjacent IPL and SPL, activated proportionally to demands on endogenous visuospatial attention, consistent with previous studies reporting activation of the IPS, predominantly in the left hemisphere, by cue-induced orienting [90,93,122]. Frontal regions displaying activation patterns consistent with endogenous control were located in the MFG, and tended to be larger in the left hemisphere [90,173]. The bilateral TPJ, the cingulate gyrus, the right precentral gyrus, and the anterior and posterior insula, the bilateral fusiform gyri, the lingual gyri, and the cuneus displayed responses to targets that increased with their spatial unpredictability, indicating engagement by stimulus-driven orienting. These results were interpreted in favor of the idea of two largely dissociated neural networks mediating endogenous and stimulus-driven control of visuospatial selective attention.

Using an event-related approach, Kincade et al. [174] compared the brain activations produced during the cue and target periods in response to endogenous, exogenous, or neutral cues. During the cue period, fronto-parietal regions, including the bilateral FEF, the IPS, extending into the SPL, and the occipital lobe, responded mostly for endogenous cues. The right TPJ and IFG also responded more for endogenous vs. exogenous cues, although the response was two seconds delayed with respect to the dorsal network. During the target period, the right TPJ and the right FEF were activated after invalid endogenous cues, but not after invalid exogenous cues. This study confirmed the importance of the dorsal fronto-parietal system in endogenous orienting. Exogenous orienting to the color singletons used by Kincade et al. appeared to involve a partly overlapping circuit comprising regions in the extrastriate visual cortex that may mark a location, and dorsal frontoparietal regions, such as the FEF, to direct attention. Exogenous orienting, however, did not seem to recruit the TPJ portion of the ventral system, indicating that the TPJ might only be involved in stimulus-driven shifts if the stimuli share features that are behaviorally relevant (contingent orienting). The nearly complete absence of brain activations observed during exogenous orienting observed in Kincade et al.'s study might however be explained by the absence of behavioral effects produced by the exogenous cue in the fMRI design,

in which cue-to-target SOA was increased to 2 s. The insufficient temporal resolution of fMRI prevents the capture of fast and brief cerebral events, such as exogenous attentional orienting, which peaks ~100 ms after cue onset [29].

Other studies demonstrated that the ventral network is not recruited by orienting to non-predictive but salient cues presented before a target appears. Similarly, uninformative but salient distracters that attract attention do not activate the ventral system, although they did activate the dorsal system [118]. This might suggest that exogenous orienting recruits the same dorsal frontoparietal network that is responsible for directing attention based on goals or expectations. The ventral network is not activated by orienting to distinctive but unimportant stimuli (exogenous orienting), except perhaps in the special case where observers do not have an ongoing task, but it does underlie reorienting to environmental stimuli based on their task relevance [118]. According to all this evidence Corbetta et al. [118] have recently concluded “[...] that the psychological distinction between exogenous and endogenous orienting [34] may not map onto different neural systems. Rather, a more fundamental distinction appears to be between systems involved in orienting, both exogenous and goal-driven, i.e., the dorsal attention system, and those involved in stimulus-driven reorienting, i.e., the ventral and dorsal attention systems”.

It is however difficult to conceive that systems, which are clearly differentiated in their behavioral effects, do not map onto distinct neural substrates. We believe it is much more likely that the limited temporal resolution of fMRI constrains the neuro-anatomical conclusions. Relevant neuropsychological evidence from right parietal damage patients, for example, indicate that such lesions are associated to impairments in contralesional exogenous orienting, with a relative sparing of endogenous orienting [70], thus strongly suggesting the anatomical segregation of those two systems. Friedrich et al. [175] reported extinction-like patterns (related to exogenous orienting) for contralesional targets in patients with damage to the TPJ, with larger effects in non-parietal than in parietal patients, hence emphasizing the role of parietal regions in the attentional disengagement of endogenous orienting [132]. Brain lesions specifically affecting endogenous attention are more difficult to find, maybe because the endogenous attentional system is bilaterally distributed in the fronto-parietal cortex, a brain lesion that is less likely to be produced. Patients with Bálint syndrome, who typically have difficulties in voluntarily directing their gaze in space, have bilateral lesions in the occipito-parietal cortex [176,177], although the evaluation of spatial attention is highly difficult due to simultagnosia and ocular apraxia. There are also suggestions in the literature that patients with prefrontal cortex damage have problems with endogenous orienting [178–180]. Perhaps the dorsal attentional networks need to interact with more rostral sectors of prefrontal cortex in order to “remember” the context of the task and properly take into account the predictive value of the cues.

The temporal resolution and causal power of event-related TMS has recently been used to explore the implications of key dorsal and ventral parietal regions in endogenous and exogenous attention [181]. TMS was used to interfere in a trial-by-trial basis with the IPS and TPJ in the right hemisphere during the orienting period, i.e. before target presentation. Results showed that the right IPS was involved in both types of orienting, while the right TPJ was implicated in the orienting of exogenous, but not endogenous, spatial attention. In particular, TMS over both the right IPS and TPJ produced an abnormal facilitation instead of IOR at long SOAs when non-predictive peripheral cues attracted attention exogenously. When predictive peripheral cues were used to encourage endogenous orienting, only right IPS stimulation induced an abnormal facilitation at long SOAs, which was not observed in the sham control condition or when the right TPJ was stimulated. Therefore,

at least part of the ventral fronto-parietal network (right TPJ) does participate in exogenous attention, and not only in stimulus-driven reorienting to unattended targets as suggested by previous fMRI studies [174]. Future research using TMS and other methods with high temporal and spatial resolution will hopefully determine further anatomical dissociations related to endogenous and exogenous orienting.

Finally, endogenous and exogenous orienting might differ not only in the brain structures involved in the control of each system, but also in the timing of activations. In humans, electroencephalographic data have shown that the initial part of a sustained orienting-specific activity, beginning at 400 ms post-cue, derived primarily from the frontal cortical regions, with the parietal contribution not beginning till after 700 ms [182]. This was then followed (beginning ~800–900 ms post-cue) by pre-target biasing activity of specific visual cortical areas contralateral to the direction of attention in preparation for the to-be-detected visual target stimulus. In contrast, Green and McDonald [183] reported that following an endogenous signal to shift attention, activity was seen in the parietal cortex 100–200 ms before activity was observed in frontal cortex. Parietal cortex was then reactivated prior to anticipatory biasing of activity in occipital cortex. The magnitudes of early parietal activations were strongly predictive of the degree of attentional improvement in perceptual performance. Physiological studies indicate that the dorsolateral prefrontal cortex (PFC) and the posterior parietal cortex (PPC) show interdependence of neural activity [184], consistent with the idea that spatial attention results from the coordinated activity of fronto-parietal systems, and not of localized cortical nodes. In the monkey, PPC and PFC areas showed coordinated activity when the animal selects a visual stimulus as a saccade target. Importantly, PFC and PPC had distinctive dynamics of interaction when attention was selected by the stimulus (bottom-up or exogenous orienting) or when it is directed by more top-down (or endogenous) goals. Bottom-up signals appeared first in the parietal cortex and were characterized by an increase of fronto-parietal coherence in the gamma band, whereas top-down signals emerged first in the frontal cortex and tended to synchronize in the beta band [184].

## 5. Concluding remarks

In the present paper we have reviewed behavioral and neuroimaging evidence on the differential characteristics of endogenous and exogenous spatial attention, as well as their neural implementation. Accumulating behavioral evidence indicates that endogenous and exogenous attention differ not only in quantitative aspects (such as in the magnitude of the attentional effects or their time course), but also in their qualitative effects on information processing. Exogenous attention produces effects at early stages of processing, affecting stimulus enhancement as well as external noise reduction, and perceptual processing based in object coordinates. Endogenous attention, on the other hand, affects external noise reduction and perceptual processing based on spatial coordinates, also producing effects at later stages of processing. Although the behavioral dissociations suggest that endogenous and exogenous attention consists of two independent attentional systems, they sometimes interact for the control of behavior. In general, when tasks involve the discrimination, rather than detection, of target features, endogenous attention boosts the effects of exogenous orienting [47,75]. These behavioral dissociations and interactions suggest that both systems should be implemented in segregated neural substrates, but with some common (or interconnected) regions allowing their interaction.

Existing fMRI-based network models of attentional orienting in humans have set up a comprehensive framework for discussion.

They put forward the hypothesis of a dorsal frontoparietal network in the orienting of both endogenous and exogenous attention, and a ventral frontoparietal counterpart in reorienting to task-relevant events [118]. However, as reviewed above, most of the imaging studies exploring attentional orienting in space have focused on endogenous attention, which timing parameters are more easily adaptable to techniques such as fMRI. Only a few studies have directly compared the neural correlates of endogenous and exogenous orienting, but they have either not distinguished between cue and target periods [87,89,92–95,170], or they have focused on target related activity [171,172]. Only one fMRI study adapted the fMRI methodology to explore the brain regions associated to endogenous and exogenous orienting during the cue period [174]. Nonetheless, the insufficient temporal resolution of such technique prevented the capture of fast and brief cerebral events, such as exogenously driven attentional orienting. Neuropsychological studies have demonstrated that lesions of the right inferior parietal cortex and its connections with the ipsilateral frontal cortex selectively disrupt exogenous, but not endogenous orienting [68,70,141]. This hypothesis has recently been confirmed by using non-invasive neurostimulation techniques such as TMS [181]. Moreover, functional interactions between the frontal and parietal cortex also seem to differ when spatial attention is oriented either endogenously or exogenously [184].

The accumulation of behavioral dissociations on the effects of endogenous and exogenous attention gives strong support to the hypothesis that endogenous and exogenous attention consist of two independent attentional systems, with well differentiated functional characteristics. Evidence from neuroimaging studies might suggest otherwise that endogenous and exogenous attention are implemented in partially overlapping brain regions. On the other hand, neuropsychological and non-invasive neurostimulation techniques indicate that some brain regions, such as the right TPJ, are causally implicated in the orienting of exogenous but not endogenous attention. Future studies will need to make use of neuroimaging techniques with higher temporal resolution (such as magnetoencephalography) to better explore the neural correlates of exogenous orienting. Moreover, TMS has proven its efficacy for testing the causal contribution of isolated nodes in endogenous and exogenous orienting. The combined use of TMS and fMRI might provide further insight on the brain circuits that are causally implicated in either attentional system, as well as on their patterns of overlap and interactions.

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