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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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Contents

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, 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