

Reconceptualizing inhibition of return as habituation of the orienting response

KRISTIE R. DUKEWICH

Dalhousie University, Halifax, Nova Scotia, Canada

Inhibition of return (IOR) is an effect on spatial attention whereby reaction times to a target presented at a location where a stimulus had recently been presented are increased, as opposed to when a target is presented at a new location. Despite early reports that habituation is not responsible for the IOR effect, the human cognitive literature provides indirect evidence in favor of the possibility. In addition, recent neurophysiological studies provide direct support for the idea that habituation is at least a contributing source for the IOR effect. The present article describes how habituation may account for the IOR effect and explores some of the predictions that this hypothesis suggests.

Unpredictable events in peripheral vision often cause an automatic covert shift of attention to the location of the event (Posner & Cohen, 1984). The consequence of this shift of attention is that once attention is withdrawn from the exogenous event, attention is slower to return to this location than it is to deploy to a new location—an effect called *inhibition of return* (IOR; Posner, Rafal, Choate, & Vaughan, 1985). It has been proposed that IOR is a mechanism through which events at novel locations are given priority over events at a previously inspected location. The consequences of unexpected events are commonly studied using the Posner cuing paradigm, in which a target to be detected is preceded by a brief orienting event (a “cue”) that does not predict the location of the target to follow. Generally, if the cue–target stimulus onset asynchrony (SOA) is less than approximately 150 msec, people are faster to detect the target if it appears at the same location as the cue than they are if it appears at a different location—an effect called facilitation. When the SOA is greater than approximately 200 msec, this trend is reversed. It is this reverse trend that is the IOR effect (Klein, 2000).

The Posnerian description of orienting to exogenously presented stimuli and its consequences was not the first such characterization; these concepts were previously described within a physiological framework. Pavlov (1927) was the first to describe the orienting reflex as a product of an organism’s directing the appropriate receptor organs toward novel events in the environment. The orienting response is subject to habituation—a decrease in the magnitude of the orienting response with repeated presentations of a stimulus that is not paired with an outcome. A variety of physiological changes occur when an organism detects a novel stimulus, including pupil dilation, the electrodermal response, a pause in respiration, and

vasoconstriction in the periphery, among others (Barry, 2006). Although these changes are not perceptual, what these changes represented was considered perceptual by Sokolov (1963), who provided a conceptual theory of the orienting response and its habituation. In his comparator theory, Sokolov described the orienting response as the major unit of perceptual functioning. He proposed that the presentation of a novel stimulus generates a representation of the stimulus preattentively, at the neuronal level. Incoming stimuli are compared with this model, and if there is a mismatch, an orienting response is generated. This response is graded, so that the greater the mismatch, the greater the orienting response. With repeated presentations of the same stimulus, the neuronal model becomes an increasingly more accurate representation of the real stimulus, resulting in a continuously smaller orienting response with each stimulus presentation. A change in any aspect of the stimulus in relation to the “model” will evoke a new orienting response, even the omission of a stimulus presentation.¹ This suggests that Sokolov’s conception of the neuronal model contains all parameters of the stimulus, including its temporal characteristics.

Given the shared topic of interest, it is unclear why cognitive researchers have been reluctant to explore some of the attentional concepts developed in the physiology literature. Perhaps one reason is based on the fact that the physiological descriptions of orienting and its habituation tend to rely on involuntary indices of attention. Posner, Snyder, and Davidson (1980) argued that although Sokolov (1963) and others (see, e.g., Miller, Morse, & Dorman, 1977) had interpreted these measures in a perceptual way, changes in involuntary indices of orienting—such as the galvanic skin response—were too slow to allow precise specification of the timing of perceptual awareness. Presumably, reaction times (RTs) are not subject to this criticism, since

K. R. Dukewich, dukewich@dal.ca

they are assumed to temporally correlate with perceptual awareness. There are other differences in methodology and interpretation that might have contributed to keeping these two literatures separate from each other. I believe that their similarities are underappreciated. In agreement with Cowan (1988), who suggested that cognitive psychology would benefit from a greater attention to the concept of habituation, in the present article I plan to show the potential of reconceptualizing inhibition of return as habituation of the orienting response.

Whatever the reason for the enduring lack of connection between the cognitive concept of IOR and the physiological concept of habituation, these two concepts are at least superficially reminiscent of each other. The present review will attempt to reconnect these literatures. First, the characteristics of habituation are discussed, and an attempt is made to describe IOR within a habituation framework. This is followed by a review of the neurophysiological evidence relevant to orienting, IOR, and habituation that together suggest IOR is due—at least in part—to a decrement in a response with repeated stimulation of the same neurons. I also include a discussion of the role of sensory adaptation in habituation, and its possible involvement in explaining simple, but not complex, forms of IOR. Next, I review some findings from the IOR literature that may seem inconsistent with a habituation account and attempt to show how they may be reconciled with this account. Finally, I describe some of the specific predictions that this hypothesis provides, and conclude with suggestions for future research.

Habituation Recovered

In the past decade, many researchers have assumed that IOR is a form of working memory (Birmingham & Pratt, 2005; Boot, McCarley, Kramer, & Peterson, 2004; Castel, Pratt, & Craik, 2003; Klein & Dukewich, 2006; Paul & Tipper, 2003; Shore & Klein, 2000). Evidence has emerged to both support (Castel et al., 2003) and refute (Theeuwes, Van der Stigchel, & Olivers, 2006) the involvement of working memory in the expression of IOR; however, the intended connotation of the term *working memory* is unclear and probably varies depending on the context. Although the IOR effect could be described as working memory for an ignored location, an alternative description could just as easily couch IOR in terms of learning.

Implicit learning is broken down into two forms: non-associative and associative. Forms of associative learning, such as classical or operant conditioning, inform the organism about the relationship between two stimuli or between a stimulus and a behavior. Forms of nonassociative learning, such as habituation and extinction, inform an organism about a specific stimulus. In general, contiguity between a stimulus and the outcome supports the development of associative learning, whereas a lack of contiguity supports the development of nonassociative learning (Escobar & Miller, 2004). In Posner's exogenous cuing paradigm, the cue is nonpredictive (i.e., the target location is not contingent on the cue location); thus, it is likely to invoke a nonassociative learning mechanism, such as habituation.

Habituation has been described as an adaptive response that allows animals to redistribute limited processing resources away from events that are repetitive or familiar (Stephenson & Siddle, 1983)—an explanation reminiscent of Posner et al.'s (1985) "novelty seeking" proposal for IOR. The phenomenon is generally described as a process that happens to the orienting response and is based on some characteristic(s) of a stimulus; with repeated presentations, the orienting response habituates to the stimulus.

In a classic review of the earlier literature, Thompson and Spencer (1966) outlined several critical characteristics of habituation. Specifically, an irrelevant stimulus will elicit a decremental response with repeated presentations of a stimulus (habituation). The decrement is greatest in the first few presentations, and then it slows down. The rate and extent of habituation increase as the rate of stimulus presentation increases and as the intensity of the stimulus decreases. Highly intense stimuli may not elicit any habituation. Habituated responses will recover over time following the cessation of stimulation, referred to as *spontaneous recovery*, and they are susceptible to *dishabituation*—a return to previous levels of responding following the presentation of another, usually strong, stimulus. Habituated responses also show *generalization*: Stimuli that are similar to the stimulus used to generate habituation will also elicit an attenuate response, as opposed to prehabituation levels of responding. Figure 1A illustrates several of these critical characteristics using a general example of a response that shows habituation. Thompson and Spencer argued that "examples of habituation can probably be found in essentially all behavioral studies where a stimulus is regularly presented" (p. 18). Indeed, habituation is so ubiquitous, it can be seen at virtually every level of response (Rose & Rankin, 2001). Figure 1B illustrates the habituation function for two stimulus presentations coupled with the spontaneous recovery function.

The time course of habituation is a critical factor in an effort to relate this phenomenon to IOR as it is typically studied. IOR is a relatively rapid effect, appearing approximately 250 msec following the presentation of a single cue (Klein, 2000), and dissipating within 3,200 msec (Samuel & Kat, 2003; but see Dodd & Pratt, 2007b, for evidence of IOR as early as 30 msec after the onset of the cue and lasting 6 sec). How rapidly habituation can be observed depends on a variety of factors (Thompson & Spencer, 1966), including the stimulus duration, the interstimulus interval (ISI), and the duration of the response. In most IOR studies, all of these variables are extremely short: Cues are typically presented for less than 100 msec; the ISI, or more commonly the cue-target onset asynchrony (CTOA), is rarely longer than 1,200 msec, and exogenous visuospatial orienting, as evidenced by early facilitation, is extremely rapid and transient. There is evidence that habituation in the human cortex can act within seconds (Yamaguchi, Hale, D'Esposito, & Knight, 2004), but I have been unable to find any habituation-focused studies that have demonstrated a time course for habituation as short as that observed in IOR. This is hardly evidence against the habituation hypothesis, given that ISIs as short

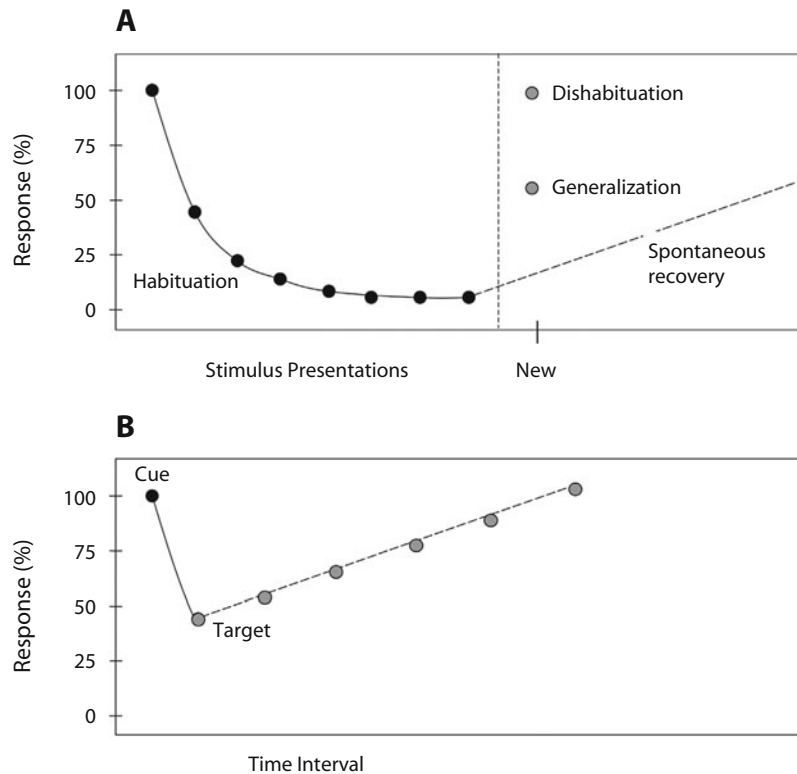


Figure 1. (A) A schematic representation of some of the typical characteristics of habituation. See text for details. (B) To account for IOR, the habituation function must be reduced to the first two stimulus presentations (i.e., cue and target), with the spontaneous recovery function moved to the end. This transforms the x-axis from number of stimulus presentations to the time interval between stimulus presentations. If one varies the time interval between the cue and the target, the target reveals the spontaneous recovery function. This predicted pattern of results is strikingly similar to the pattern illustrated in Samuel and Kat's (2003) graphic meta-analysis of the time course of IOR.

as those employed in IOR have not been exploited in traditional studies of habituation. As such, IOR might be interesting to psychophysicists precisely because of its rapid appearance. In any event, the rapid onset and dissipation of IOR is not inconsistent with how habituation has been characterized thus far.

The fact that facilitation is longer lasting in the target-discrimination studies than in target-detection studies (Lupiáñez, Milan, Tornay, Madrid, & Tudela, 1997) suggests that the orienting response is longer in the former, leading to a later onset for habituation. In detection tasks, one only needs to process that a target has been presented. In discrimination tasks, one needs to process the target presentation and then the target identity, which will extend the duration of the orienting response and thereby delay the onset of habituation (see Lupiáñez, Milliken, Solano, Weaver, & Tipper, 2001, for a similar explanation). Variations in the duration of the orienting response can also be used to explain why a cue at fixation following the presentation of a peripheral cue tends to improve observations of IOR (MacPherson, Klein, & Moore, 2003; Prime, Visser, & Ward, 2006). A cue back to fixation terminates the orienting response generated by the peripheral cue, hasten-

ing the onset of IOR. The reason IOR is generally more reliable with a cue back to fixation is because IOR onset is going to vary tremendously between participants; a cue back to fixation will artificially force everyone's orienting response to terminate at around the same time.

Taylor and Klein (2000) argued that early facilitation observed in Posner cuing experiments is inconsistent with habituation; however, for a response to exhibit habituation, an organism must first produce it. In the case of IOR, the response presumed to be habituated is attentional capture, based on the repetitive stimulation of a single location in space. In order to map the existing IOR literature onto a theory of habituation, the facilitatory effects of exogenous cues must be considered in conjunction with the inhibitory effects. An exogenous cue produces an orienting response so that perceptual processing at the cued location is initially enhanced (i.e., facilitation). Thus, in contrast with the supposition of Taylor and Klein, early facilitation is the hallmark of the orienting response.

When the cue and target are both presented at the same location, the response to the target will always be smaller than the response to the cue. At both short and long SOAs, the orienting response generated by the target builds on the

orienting response generated by the cue. However, when the SOA is short, the orienting response generated by the cue has not had time to dissipate, so the summation of the cue response to the target response produces a greater level of overall activation. At longer SOAs, the orienting response generated by the cue has time to dissipate, so the summation produces less overall activation. It is the peak of the summed cue and target activation that dictates the speed of response to the target. See Figure 2 for a schematic representation of the habituation hypothesis, using a hypothetical continuous attentional response.

It should be noted that aspects of this characterization of IOR are not entirely novel. Lupiáñez and Milliken (1999) and their colleagues (Lupiáñez et al., 2001; Lupiáñez, Ruz, Funes, & Milliken, 2007) have described IOR in terms

of object-file integration (see Kahneman, Treisman, & Gibbs, 1992), in which current perceptual information is integrated with the memory representations of prior experience. They emphasize that on uncued trials, the onset of the target is spatially distinct from the onset of the cue; on cued trials, the lack of spatial distinctiveness encourages the integration of the two events (Lupiáñez et al., 2007). These ideas are all inherent in the habituation account and share considerable overlap with Sokolov's (1963) comparator theory of habituation. The habituation account is simply a more parsimonious description that relies on previously established concepts from physiology.

Both early facilitation and late IOR are incredibly robust phenomena. The fact that the cues do not seem to stop causing some amount of orienting is puzzling: How does

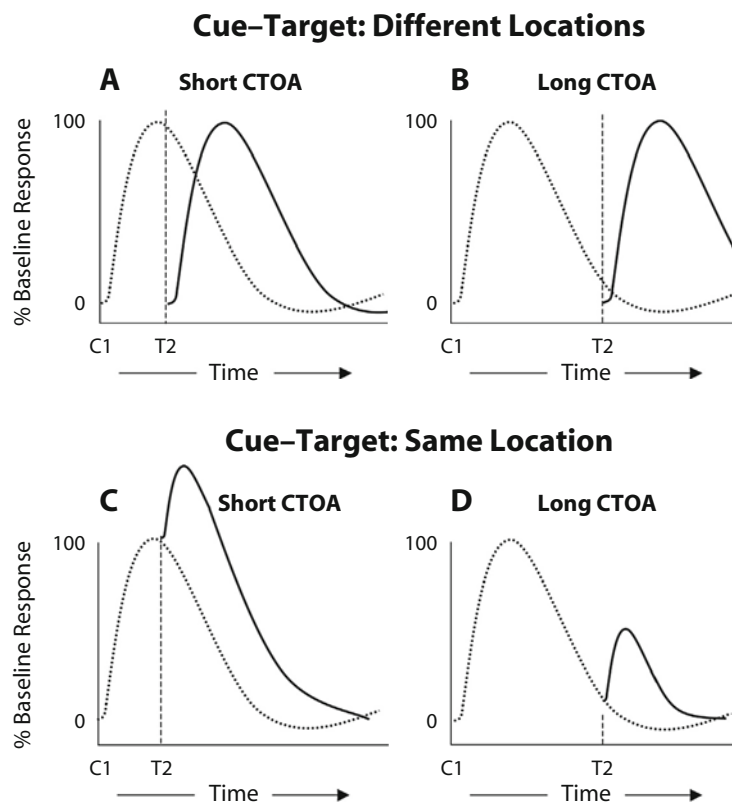


Figure 2. A schematic representation of IOR as a product of habituation. In all panels, the response being measured is a hypothetical continuous response that can represent either the sensory component or the motor component of the orienting reflex. It is location specific and peaks shortly after the presentation of the cue (C1). Note that this response is consistent with an uncued minus cued conversion of RTs that is often interpreted to represent attention. Baseline is the peak response to a single stimulus at a single location. The dotted line represents the orienting reflex generated in response to the cue, presented at C1, whereas the black line represents a second orienting reflex generated in response to the target, presented at T2. In (A) and (B), the T2 response is independent of the C1 response because they are generated at different locations. In (C) and (D), the T2 response is 40% smaller than the original C1 response because they are generated at the same location. When the interval between the cue and the target is short (C), the reduced attentional response generated by the target builds on the attentional response generated by the cue, resulting in a larger response than baseline. When the interval is long (D), the reduced response generated by the target is left to fend for itself, resulting in a smaller response than baseline.

the IOR accumulated within a trial get reset? In all likelihood, it does not. Consider a standard IOR paradigm: The baseline (the *y*-axis, as depicted in Figure 2) is the average RT to targets presented at a cued location as opposed to an uncued location. Across trials, habituation of location may accumulate. However, researchers are typically very careful to present equal numbers of cued and uncued trials, as well as equal numbers of cues and targets at both the left and right locations. Therefore, any accumulated habituation will be equivalent for both locations, and on a given trial, the most recent cue will result in greater habituation at the cued location than at the uncued location. That is, if the *y*-axes in Figure 2 are all adjusted to represent 50% of baseline responding—as might be the case in the final blocks of a single experimental session—then the relative relationships of each of the responses are all still maintained.

Critically, the role of habituation in IOR is along a single dimension: space. The cue and target used in a typical Posner cuing task have different identities, so the repetition that accounts for the IOR effect is presumably based primarily on location. This suggests that habituation operates on a more specific level; only the relevant feature(s) of a stimulus will habituate. This characterization is consistent with the way in which the developmental literature has exploited habituation to examine infant categorization (Cohen, 2004). Developmental studies of infant categorization often habituate infants by repeatedly presenting objects from a category of stimuli, such as cats (Spencer, Quinn, Johnson, & Karmiloff-Smith, 1997) or animate objects (Legerstee, 1992), using exemplars that vary tremendously in their physical representations. In these experiments, habituation is based on the repetition of a concept or category, rather than on the perceptual attributes of the stimuli. This characterization of habituation is also consistent with emerging evidence that only changes in the relevant dimension are critical for producing re-inspection (Lleras, Rensink, & Enns, 2007). Although this evidence is not specifically about orienting and habituation, it is conceptually similar enough to suggest that habituation and novelty can be relative, on the basis of only one aspect of a stimulus.

Although space is the dimension along which habituation is acting, IOR is unique because space is an attribute of both the stimulus and the orienting response.² In most IOR experiments, the cue is either black or white (depending on the background color used). The location of the cue is a sensory attribute, as is its color. However, the motor component of the orienting reflex is also spatial. This is not an issue with something like color; there is no white motor response or black motor response, because color is purely perceptual. So does space belong to the stimulus or to the response? In all likelihood, space is an attribute of both the stimulus and the response. Given that habituation can act at virtually all levels of processing (Rose & Rankin, 2001), it is probable that habituation in an IOR paradigm is affecting both the sensory processing of the target on the basis of the sensory processing of the cue and the reflexive motor response to the target on the basis of the reflexive motor response generated by the cue.

Indeed, IOR has been shown to be sensory and attentional, as well as motor and oculomotor (see Berlucchi, 2006, for a review), consistent with how habituation should be applied to the IOR effect. Posner and Cohen (1984) initially described IOR in terms of sensory processing, but subsequently reconceptualized it in terms of attentional orienting (Posner et al., 1985) following the publication of evidence that IOR was not based on sensory habituation (Maylor & Hockey, 1985). Subsequent results from Rafal, Calabresi, Brennan, and Sciolto (1989) found evidence of IOR generated at locations without sensory stimulation following the preparation of an eye movement. They used these results to argue that IOR is caused by oculomotor preparation in response to a peripheral or centrally presented cue. These seemingly contradictory findings can all be accounted for if habituation is acting on space as an attribute of the stimulus, the response, or both.

Furthermore, space is not solely a sensory attribute in the way that color is. If people can keep track of things moving in space, then there is some place in the brain that is performing this function. That place, in all likelihood, is subject to habituation the same as any other area in the brain. To distinguish these levels of spatial processing as they apply to the stimulus, I will refer to higher order treatments of space as categorical rather than sensorial.

A Return to Physiology

On the basis of neuropsychological investigations, the superior colliculus (SC) was identified as a neural structure that is particularly important for both orienting and the IOR effect (Posner et al., 1985; Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988; Sapir, Soroker, Berger, & Henik, 1999). Located in the dorsal midbrain and situated just beneath the posterior cerebral cortex, the SC receives afferent inputs from the cortex, inferior colliculus, retina, and spinal cord, and sends efferent outputs to the paramedian pontine reticular formation and spinal cord to generate orienting motor commands (May, 2005). Histological staining has revealed a laminar structure, with the superficial layers involved in the processing of spatial information on the basis of visual signals, whereas the deeper layers receive signals from vision, audition, and tactile sensations, allowing multisensory representations of space (May, 2005; Wallace, Wilkinson, & Stein, 1996). Ablation studies in cats (Burnett, Stein, Chaponis, & Wallace, 2004; Lomber, Payne, & Cornwell, 2001), rats (Overton & Dean, 1988), and hamsters (Thinusblanc, Scardigli, & Buhot, 1991) have demonstrated a causal link between activity in the SC and the production of orienting behaviors and responses to novelty. For example, Lomber et al. (2001) unilaterally deactivated the superficial layer of the SC in cats and found profound orienting deficits for both moving and stationary visual stimuli presented in the contralateral hemispace. When the deactivation was extended to include the intermediate layers of the SC, the animals also began to neglect auditory stimuli presented in the contralateral hemispace. Both deficits were eliminated when the cooling deactivation was reversed, demonstrating that the SC is involved in the orienting of the eyes, ears, and head toward a novel

stimulus in the environment (see, e.g., Corneil, Olivier, & Munoz, 2002; Lomber et al., 2001; Meredith & Stein, 1996; Sparks & Nelson, 1987).

The most direct evidence for a decremented response as a function of repetition comes from recent extracellular recording experiments. Dorris, Klein, Everling, and Munoz (2002) were the first to show that the delay in saccadic RTs that is typical of IOR is associated with a reduction in the magnitude of the target-aligned activity, whereas Fecteau and Munoz (2005) showed that the early facilitation that is often observed with short SOAs corresponds to an increase in target-aligned activity. On short SOA trials, the target appears within the window of the sensory signal generated by the cue, so the target-aligned activity is able to build on the signal (see Figure 2C), resulting in a faster saccade (Dorris, Paré, & Munoz, 2000). At longer SOAs, the activity level of the neuron in the interval immediately preceding the presentation of the target was higher, but the incoming target-related activity was weaker, resulting in a delay to reach threshold to produce a saccade (Fecteau, Bell, & Munoz, 2004). Fecteau and Munoz went on to expand these results to show that although visual neurons located in the superficial layers of the SC (SCs) and visuomotor neurons in the intermediate layers of the SC (SCi) were both affected by the appearance of a cue before the target, activity in the visuomotor neurons showed a stronger correlation with behavior.

Taken together, these results show there is a decrement in responding of SCi neurons with repeated stimulation that is consistent with habituation. Although all of these studies have used a more traditional Posner cuing paradigm with a single cue and a single target appearing at either the same or opposite locations, this group has begun to experiment with multiple cues in order to specifically examine habituation and sensory adaptation in the SC (Boehnke, Itti, & Munoz, 2006). Early results from these experiments suggest that SCs neurons show immediate reduction in responsivity after the first cue without a further reduction in neuronal activity with more cues; however, SCi neurons show an exponential-like decrement in activity with repeated stimulation. Boehnke et al. have attributed these effects to adaptation and habituation, respectively.

Most neuroscientists investigating IOR have focused on the SC, but any area of the brain shown to be involved in the processing of spatial information is a candidate for a neuroanatomical correlate of IOR. For example, in primates, the intraparietal area of the posterior parietal cortex has been identified as a key structure for external representations of space. Neurophysiological studies have shown that this area is organized into overlapping auditory and visual RFs (Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005). The posterior parietal lobe has also been implicated in the spatial processing in humans. Damage to the posterior parietal cortex can result in unilateral neglect—a condition whereby patients systematically ignore the contralesional side of space (Vallar & Perani, 1986). In addition, some behavioral data support the notion that IOR involves both cortical and subcortical substrates (Sumner, 2006; Tipper et al., 1997). Given that

habituation can occur at every level of response (Rose & Rankin, 2001), “where” in the nervous system the orienting is computed is not as important to my argument as “how” these computations are affected by repetition of the orienting-causing events.

Adaptation and Habituation

Sensory adaptation is a reduction in the effectiveness of a stimulus to elicit a response from a sensory receptor or neuron (Kohn, 2007). Both adaptation and habituation will produce a decrement in neuronal response with repeated stimulation; however, adaptation is about neuronal fatigue, whereas habituation is about learning to ignore an irrelevant stimulus. Cognitive psychologists might justifiably argue that IOR cannot be due to sensory adaptation alone, since there is a mountain of evidence to suggest that IOR is not confined to the sensory receptors of the retina. For example, Maylor and Hockey (1985) showed that when participants moved their eyes between the presentation of the cue and the target, IOR was observed at the environmental location of the cue. In addition, Tassinari and Berlucchi (1993) showed that a cue presented to one eye can induce IOR as measured by presenting the target to the other eye. These and other results (see, e.g., Bennett & Pratt, 2001) all point to the fact that IOR is not generated at the retina. However, neurophysiologists might argue that sensory adaptation is not an effect that solely acts on the sensory receptors; rather, sensory adaptation can affect sensory processing areas in the cortex and subcortex, and might even be more pronounced in the cortex in which receptive fields are larger (Kohn, 2007). If one accepts that adaptation is operating in the cortex, then it becomes difficult to disentangle habituation from adaptation.

In vivo, sensory-based habituation in most cases reflects a combination of both habituation at higher levels of the central nervous system, and adaptation of sensory receptors and sensory neurons (Wang, Walker, Sardi, Fraser, & Jacob, 2002). Wang et al. distinguished sensory adaptation and habituation in humans by correlating physiological event-related potential (ERP) responses with psychological reports of odor perception and found a separate time course for each, with habituation to odor occurring 50% faster than receptor adaptation. In contrast, Yadon and Wilson (2005) found that animals that were administered a receptor antagonist to prevent adaptation in the primary olfactory cortex showed less habituation of exploratory behavior toward a novel stimulus than did control animals. Taken together, these findings suggest that sensory adaptation at the receptor and in the cortex help to inform overt forms of habituation, but that habituation must also rely on more central, nonsensory related processes.

Whether the decrement in response of neurons in the SC and elsewhere in the brain represents adaptation or habituation has yet to be determined; in all likelihood, both processes are involved. Simple forms of IOR, like those studied using extracellular recordings in primates, could possibly be explained by sensory adaptation on the basis of the spatial location of stimulation. The need to invoke habituation at all is based on two lines of evidence. First,

when a cue is made predictive in a Posner cuing paradigm, behavioral IOR is reduced. There has also been evidence that this effect is mirrored in the response of neurons in the SC: Predictive cues elicit a significantly smaller decrement in the neuronal response with repeated stimulation than do nonpredictive cues (Fecteau & Munoz, 2005). This finding is inherent in a model of habituation, but is not accounted for by a model of sensory adaptation. Second, some incarnations of IOR suggest that space is being treated as a category rather than as a primary sensory attribute. Simpler forms of IOR might be accounted for using a model of adaptation in retinotopically organized pathways (including, of course, the SC), whereas findings of environmental, object-based, and cross-modal³ IOR cannot be. These forms can, however, be explained by habituation operating at a categorical level of processing. For example, Tipper, Driver, and Weaver (1991) demonstrated that when an object that appeared to rotate on a computer screen was cued, the IOR associated with the cue moved with the object, rather than remaining exclusively at the environmental coordinate. Spence, Lloyd, McGlone, Nicholls, and Driver (2000) investigated every possible combination of modality for cue and target, using auditory, visual, and tactile stimuli, and found IOR regardless of differences between the modality of the cue and target (Lyons, Glazebrook, Keetch, Dhillon, & Elliott, 2006; Spence & Driver, 1998; Spence et al., 2000). These findings imply that IOR is capable of being generated at some distance from the sensory organs and primary sensory cortices.

In all likelihood, adaptation informs habituation; a change in signal from an adapted neuron—in the direction of either more adaptation or less adaptation—indicates a change in stimulus to higher order neurons. This is presumably why Yadon and Wilson (2005) found less habituation when cortical adaptation was prevented than when it was not. A change in the adapting signal results in an orienting response; over time, a lack of change results in its habituation. However, the level at which the decrement in the orienting response is going to be implemented—at either the sensory or the category level—will depend on the complexity of the stimuli and perhaps on the nature of the task. In cases in which the sensory information is never constant, habituation is obviously not proceeding on the basis of adapting space-based sensory inputs. These proposed relationships are illustrated in Figure 3.

Accounting for Inconsistencies

Although the habituation hypothesis can account for much of the IOR literature, there are several findings that might be considered inconsistent with this hypothesis. However, whether these findings are truly inconsistent with habituation depends, in part, on how one defines IOR. If IOR is simply used to refer to any instance in which people are slower to respond to targets at previously cued locations, then IOR will be everything from participant strategy and decision criteria to working memory, perceptual and motor processing, and the kitchen sink, all depending on the stimuli and methods used. But if IOR is a specific mechanism, generated by uninforma-

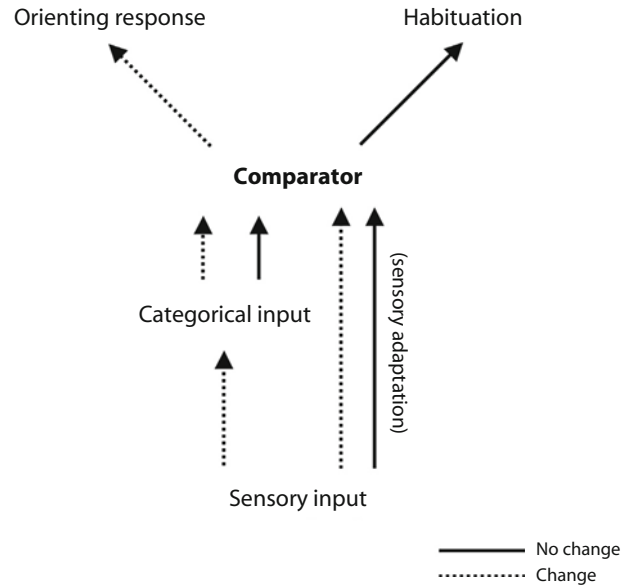


Figure 3. A schematic diagram depicting the proposed relationship between adaptation and habituation. Adaptation acts to inform habituation when habituation is proceeding along sensory-related dimensions. When the sensory inputs are constantly changing, habituation is acting at a higher-than-sensory level of analysis. Changes in input at either level will produce orienting; lack of change will result in habituation.

tive, exogenously presented stimuli, that acts to bias attention toward novel locations, then it is quite reasonable to construe IOR as habituation. I think this latter definition is what comprises most of the results described in the IOR literature, whereas the effect-based definition makes a common mechanism unlikely. Indeed, an effect-based definition makes inconsistent results—such as evidence for and against the involvement of working memory in IOR—impossible to reconcile; they would be fundamentally different effects that simply share the same name.

Researchers who use the effect-based definition of IOR will probably see the habituation account as one of many possible mechanisms for IOR. In that case, it is possible that habituation contributes to the effect only under some conditions; under other conditions, habituation might not play a role in that IOR at all. However, regardless of whether one thinks IOR is a mechanism or an effect, the point of any restrictions in the theory is to help identify when habituation is and is not responsible for IOR. The suggestion that I am advancing in the present article is that the mechanism underlying IOR-like effects generated using a Posner-style cuing paradigm is habituation. It remains to be seen whether habituation will also underlie IOR-like effects observed using paradigms that depart substantially from a spatial cuing paradigm.

I think that reports of long-term IOR might be outside of the purview of the habituation proposal. An example of this finding comes from Tipper, Grison, and Kessler (2003), who used faces to mark two possible stimulus locations to induce a more robust encoding of the events for later retrieval. A red circle presented over one of the two

faces was used as the cue, and a green circle presented over one of the two faces was used as the target. They found evidence of delayed responding to cued locations using CTOAs of 1,800 msec, 3 min, and 13 min. This range of CTOAs might place this study, and others like it, in a category far enough outside of traditional IOR so as to constitute an entirely different effect. However, Tipper et al. (2003) explicitly stated, "It is important to note here that we are not proposing inhibition of internal representations lasts for long periods. . . . However, we propose that transient inhibitory states are encoded into memory along with the associate event and may be reinstated after long delays given appropriate retrieval cues" (p. 19). This statement suggests that it is not IOR, but memory for previous inhibitory states, that produces the effect.

Several types of findings attributed to IOR that deviate from the classic Posner cuing paradigm may, at first glance, sound inconsistent with the habituation hypothesis. However, on closer examination, at least a few of these findings might, in fact, be consistent with the habituation hypothesis. Taylor and Klein's (2000) experiment can be used to exemplify how these findings may be consistent with habituation; but similar findings of IOR following an endogenously generated eye movement (Rafal et al., 1989; see also Frischen, Smilek, Eastwood, & Tipper, 2007) may also be explained by the habituation hypothesis in the same way. Taylor and Klein had their participants ignore or make a manual or saccadic response to a first stimulus (S1), and then make a manual or saccadic response to a second stimulus (S2). In each block of trials, the first and second stimulus could be an arrow at fixation or an event in the periphery. They found IOR in response to an arrow (S2) at fixation, as long as an eye-movement response was made to either S1 or S2. In contrast, in blocks for which no eye movements were made, IOR was only observed if S2 was an event in the periphery. As was noted earlier, habituation can happen in any neuropsychological system. In addition, I have already argued that space is an attribute of both the stimulus and the orienting response. Although this type of paradigm lacks the exogenous stimulation in the periphery, which comprises the stimulus component of IOR (i.e., there is a stimulus presented at center, but the IOR is observed in the periphery), the habituation proposal accounts for delayed responding in the presence of previously activated pathways. For these cases, the habituated pathways are in the motor system rather than in the perceptual system. In an extension of Taylor and Klein's interpretation of IOR, it might be that when the oculomotor system is inhibited, the habituation is primarily perceptual or attentional, whereas when the oculomotor system is activated, the habituation is primarily motoric.

There are other findings in the IOR literature that one might consider inconsistent with the habituation hypothesis. Descriptions of habituation suggest that any change in the stimuli will elicit dishabituation—a return to previous levels of orienting (Sokolov, 1963). Because IOR appears to be habituation acting on the dimension of spatial location, it is not clear whether a change along that dimension will produce dishabituation. Certainly, there is

evidence to suggest that this is not the case. For example, Danziger, Kingstone, and Snyder's (1998) finding that IOR can occur at multiple successive locations appears inconsistent with this notion. As was originally proposed by Danziger et al., Snyder and Kingstone (2001) subsequently demonstrated that IOR was only generated when participants were forced to allocate attention to the cues to confirm their nontarget identity. When the target was made predictable by blocking the number of cues before the target, and when enumeration could be kept track of by attending to a central counter, multiple tags of IOR were abolished.⁴ When each stimulus holds the potential to be a target, individual locations may be habituated independently. An analogous effect would be produced by presenting multiple color blocks sequentially to participants. Habituation can occur for each of the colors presented, so why not for multiple locations?⁵ The dissipation of the IOR effect—so that with successive cues, the first location cued shows the least amount of IOR—can be accounted for by spontaneous recovery. Using the color example, an observer can habituate to multiple colors, but the further back in time a color was presented, the less the habituation that is going to be observed for that color.

Further research (like that suggested in the next section) will be needed to fully understand how well discrepancies like these might be accounted for within a habituation framework, or whether they might require alternative mechanisms. This will involve the consideration of mechanisms that can cause cued RTs to be slower than uncued RTs, as well as of mechanisms that might counteract or mask the effects of IOR. For example, issues of visual persistence and backward and forward masking might be factors that contribute to behavioral responses to sequentially presented stimuli. A faster rate of presentation will produce more habituation than a slower rate of presentation (Rose & Rankin, 2001); however, with a faster rate of presentation, stimuli presented at the same location may not appear as discrete stimuli presented in sequence, but may instead appear as a continuously presented, possibly modulated stimulus. Under these circumstances, habituation may not be behaviorally observable at all. In addition, complex interactions between a variety of higher level cognitive strategies cannot be ignored as contributing to responses during a Posner-type cuing paradigm.

Specific Predictions

The proposal that IOR is a location-based manifestation of habituation within a trial leads to several predictions made on the basis of the critical characteristics of habituation that were outlined by Thompson and Spencer (1966). Almost no experiments have directly tested the hypothesis that IOR is a form of habituation, and results that have been used to refute a role for habituation in IOR can generally be accounted for on the basis of methods that may have been unsuitable for testing the hypothesis (see, e.g., Maylor & Hockey, 1987). In some cases, as will be shown below, the results of these experiments may actually serve to support the hypothesis. This lack of research leaves the

specific predictions of the habituation hypothesis, as of yet, relatively untested.

Prediction 1: Uninformative cues repeated at the same location will elicit a decrement in visuospatial orienting so that the IOR will increase rapidly for the first few stimulus presentations, and then continue to increase at a slower rate. The first study that attempted to directly test the habituation hypothesis with repeated cues comes from Maylor and Hockey (1987). They designed an experiment using a standard Posner cuing paradigm (i.e., one cue, one target per trial) with runs of trials that maintained the location of the cue over 1, 5, or 30 trials, while the target always appeared at a random location (see Figure 4B for an illustration). Finding no influence of cue repetition condition on IOR, Maylor and Hockey (1987) argued against the habituation hypothesis. This evidence is not definitive, however, because habituation is subject to spontaneous recovery, which may explain why the IOR effect was not more pronounced with more trials repeating the same cue location. It is also probable that as the number of cues repeated at the same location increased, the buildup of IOR at that location also increased. However, because Maylor and Hockey (1987) averaged these trials into a single cued RT and a single uncued RT, this proposed effect would have been obscured.

In support of the habituation hypothesis, Maylor and Hockey (1987) found that IOR was greater if a “same” trial was preceded by a “same” trial on the same side (i.e., the target was preceded by a cue, target, and cue all on the same side) than it was if a “different” trial was preceded

by a “same” trial (i.e., the target was preceded by a cue, target, and cue all on the opposite sides)—a result that is consistent with habituation as a model for IOR (but see Dodd & Pratt, 2007a, for a counterexample). Although they were not attempting to test the habituation hypothesis, Pratt and Abrams (1995) observed a similar result: When two successive cues were presented at the same location prior to the presentation of a target, there was greater IOR than there was when the two cues were presented at different locations (see Figure 4C). Specifically trying to test this prediction, Dukewich and Boehnke (2008) found an increase in IOR as the number of cues prior to the presentation of the target increased (see Figure 4D).

This prediction was qualified by the word “uninformative.” Given that habituation represents nonassociative learning, it is critical that the cues remain uninformative. If the cue is made predictive, then the situation moves into the realm of associative learning, which could reduce or eliminate the possibility of observing habituation. In accordance with this notion, Wright and Richard (2000) found that when the cues were made predictive, the IOR observed on “same” trials was reduced. The fact that the IOR effect was not totally eliminated could have been due to incomplete learning across trials, or it could have been due to the effect of habituation on early trials before the participant had enough experience to learn of the association.

Prediction 2: IOR will be more pronounced using a faster rate of cue presentation. Although the effect of rate of presentation for multiple cues at different locations

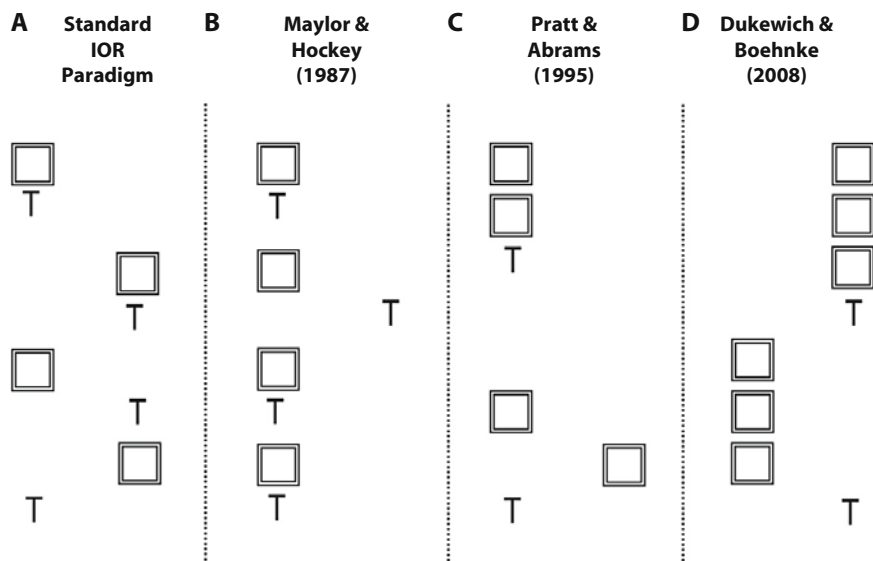


Figure 4. Different event sequences are illustrated for the typical IOR paradigm (A) and several variants (B, C, and D) that exploit multiple cues at the same location. (A) In a typical IOR paradigm, cues and targets are evenly distributed at both locations. (B) Maylor and Hockey (1987) presented runs of trials with cues at the same location (for 5, 10, or 20 trials in a row) while varying the location of the target. (C) Pratt and Abrams (1995, Experiment 1) presented two cues at the same location or two cues at opposite locations prior to presenting the target. (D) The method recommended in the present article (and used by Dukewich & Boehnke, 2008) for testing Prediction 1: Multiple cues with distinct identities (actual cues not shown) at the same location are presented prior to a target presented at the cued or uncued location.

has been investigated (Dodd, Castel, & Pratt, 2003; Dodd & Pratt, 2007b), this prediction specifically deals with multiple cues presented at the same location. Figure 5 illustrates how the rate of presentation (i.e., SOA) as well as the number of cues may affect facilitation and IOR. The hypothetical data are presented two ways: with the number of stimulus presentations represented along the x-axis (Figure 5A), as habituation researchers tend to plot the data, and with SOA represented along the x-axis (Figure 5B), as IOR researchers tend to plot the data.

Dukewich and Boehnke (2008) investigated the effect of both number of cues and rate of presentation directly using a modified Posner cuing paradigm with multiple cues, that all had distinct identities and were presented at the same location. In order to dissociate temporal predictability and spatial predictability, trials were blocked according to the number of cues presented, and a constant rate of presentation was maintained within trials.⁶ Doing so allowed participants to predict when the target would appear, but not where it would appear. In accordance with the present prediction, in Experiment 1 of their study, they found that the IOR effect increased as the number of cues increased, and that this effect was more pronounced with faster rates of cue delivery.

Prediction 3: IOR will be more pronounced when the cues are less salient. Reuter-Lorenz, Jha, and Rosenquist (1996) found an inverse relationship between IOR and target intensity (see also Castel, Pratt, Chasteen, & Scialfa,

2005); however, this prediction refers specifically to the intensity of the habituating stimulus (i.e., the cues). I know of no studies that have looked at the effects of cue saliency on IOR. Interestingly, because more salient stimuli tend to capture attention over less salient stimuli (Fecteau et al., 2004), this prediction also suggests that stimuli that elicit weaker attentional capture due to low salience will be followed by greater habituation than will stimuli that elicit more attentional capture due to high salience. This could account for IOR studies that fail to observe attentional capture before IOR. In order to test this prediction, the intensity of the cue should be varied across trials. Note that the prediction that less salient cues will be more effective at producing a decrement than will more salient cues is the opposite from what would be predicted on the basis of a theory of sensory adaptation acting alone to inform behavior.

Prediction 4: IOR will be reversed with the unexpected presentation of a change in the stimulus (dishabituation). Because I am suggesting that it is the cue that is causing habituation at the cued location, in order to dishabituate IOR, one must present an unexpected change in the cue. This may prove impossible in a single-cue/single-target type of paradigm, but may instead require multiple cues. In this vein, the finding of multiple-location IOR (Danziger et al., 1998; Snyder & Kingstone, 2001) would seem to challenge this prediction, since each cue presented at a new location constitutes a change in the stimulus. How-

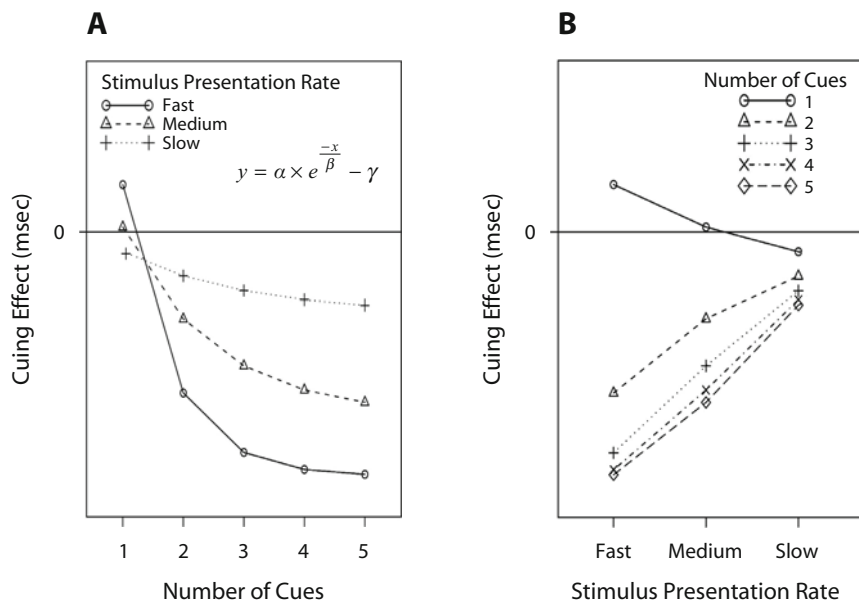


Figure 5. A generalized prediction of results on the basis of the critical characteristics of habituation and the extant IOR literature. (A) A hypothetical RT data set as a function of the number of cues presented before the target (x-axis) and the stimulus rate of presentation. The data set is based on an exponential decay function commonly observed in studies of habituation (Thompson & Spencer, 1966), with the y-intercept set by typical IOR functions (i.e., in the one-cue condition, facilitation followed by IOR, based on the rate of presentation of SOA between the cue and the target). The formula for the function (inset) has four parameters; a is a scaling parameter, β is a rate parameter, and γ is a shift parameter. (B) The same hypothetical RT data set as a function of the stimulus presentation rate (x-axis) and the number of cues presented before the target, more in line with how results in the IOR literature are plotted.

ever, I have previously argued that each cue may generate independent location-specific habituation, partially on the basis of the fact that cues presented at different locations are not unexpected in the context of that experiment. Perhaps this prediction is better tested using Thompson and Spencer's (1966) suggestion that another, strong stimulus be presented in order to induce dishabituation. In order to avoid influencing spatial attention independently from the cue, this stimulus would have to be equidistant from both possible target locations (i.e., equivalent stimuli applied to both sides of the display), or else it would have to be nonspatial. For example, either an unexpected brief flash of the entire screen or an unexpected brief tone presented through headphones might be sufficient to induce dishabituation in the spatial cuing paradigm.

Prediction 5: Repeated presentations of a dishabituation stimulus will diminish its capacity to produce dishabituation. That is, dishabituation itself can habituate. Researchers should keep in mind that Prediction 4 requires the change in stimulus to be unexpected. Pratt and McAuliffe (1999) presented multiple trials with a particular cue and target identity. In the last block, they swapped the cue and target identity to remove any previously accumulated habituation, but they failed to observe any decrease in IOR with a change in the stimuli. These findings might suggest that a change in stimulus is not capable of eliminating IOR, but in actual fact, only the first trial in the last block of trials presented an actual unexpected change to the participants. Stimuli in all of the subsequent trials in that block were entirely predictable. Although researchers will no doubt attempt to come up with a design that unexpectedly changes the stimuli, it will be an uphill battle because, almost by definition, nothing in a repeated measures experiment is unexpected.

Prediction 6: IOR will generalize to locations close to the originally cued location. This prediction suggests that there should be a spatial gradient of inhibitory strength that surrounds the originally cued location. This notion is consistent with the results of several studies that have looked at the spatial distribution of IOR showing that the strength of IOR gradually decreases as the distance between the cue and the target increases (Bennett & Pratt, 2001; Collie, Maruff, Yucel, Danckert, & Currie, 2000; Klein, Christie, & Morris, 2005; Klein & MacInnes, 1999; Maylor & Hockey, 1985; Pratt, Adam, & McAuliffe, 1998).

Prediction 7: IOR will be subject to spontaneous recovery so that performance will recover over time following the cessation of cuing. Part of the reason Maylor and Hockey (1987) may not have found an effect of cue repetition is that the interval between the cue on one trial and the cue on the following trial was at least 700 msec, and more often was closer to 1,500 msec.⁷ If the SOA is taken to represent the time course of spontaneous recovery, performance appears to recover from habituation relatively quickly. Samuel and Kat's (2003) graphical meta-analysis of IOR over a range of SOAs shows that the effect recovers gradually over time, reaching a neutral position after about 3,200 msec. As was previously mentioned, research from the habituation literature suggests that faster rates

of presentation will result in a faster rate of recovery than will slower rates of presentation (Staddon & Higa, 1996). This is exactly the opposite pattern one would predict if IOR is due to sensory adaptation acting alone to inform behavior, suggesting that rate sensitivity for spontaneous recovery should be investigated to confirm that the decrement in the IOR is related to habituation. One way to look at this would be to use a constant cue-cue SOA with multiple cues within a trial and to vary the interval between the onset of the final cue and the onset of the target.

Converging Evidence

The concept of IOR has recently been extended to include nonspatial dimensions. For example, Francis and Milliken (2003) described two forms of nonspatial IOR in vision based on stimulus length and color. Mondor, Breau, and Milliken (1998) found evidence for frequency-based auditory IOR. More recently, Morgan and Tipper (2007) have described a shape-specific version of IOR. Although these researchers did not refer to these effects as habituation, it is part of a trend of studies that have attempted to apply the concept of IOR to nonspatial dimensions (Grison, Paul, Kessler, & Tipper, 2005; Mondor & Breau, 1999; Mondor et al., 1998; Mondor & Lacey, 2001; Prime & Ward, 2002; Riggio, Patteri, & Umiltà, 2004). As I see it, there is an intuition growing among attention researchers that IOR represents a more general mechanism of attentional suppression. Habituation is likely to be the basis for this general mechanism.

Summary

Early rejections of habituation as a source of the IOR effect redirected the course of IOR research; however, much of the literature since these early claims has come to indicate that habituation and IOR are more closely related than originally thought. In the present article, I have argued that IOR is, at least in part, a manifestation of habituation on the basis of spatial location. To account for the broad and varied literature on this effect, I have used habituation in a hierarchical manner. In some cases, space is an attribute of the stimulus, and habituation is acting on perceptual pathways. In other cases, space is an attribute of the response, and habituation is acting on the motor pathways. In most cases, habituation is acting on both the stimulus and the response to produce a robust IOR effect. Habituation may treat space as a sensory attribute of the stimulus, or it may treat space as a higher order attribute, such as the environmental location stimulated or the stimulated object; the demands of the specific task will dictate which level of analysis is the most appropriate level for habituation to act on.

Habituation has largely been studied by measuring involuntary responses, such as galvanic skin response, to a repeatedly presented stimulus without requiring the subject to respond. It will be important to determine how including a stimulus that requires a response affects the characteristics of habituation. In addition, it is unclear how RT, as an index of orienting, maps onto classic measures of the orienting reflex. Characterizing this relationship will be necessary to determine whether there are differences

between how this measure and involuntary measures of the orienting response each characterize habituation.

Klein (2000) began his review of IOR by noting that orienting is a relatively primitive function in living organisms. Toward the end, he noted that

IOR is generated within a system that is normally responsible for orienting of gaze direction. IOR inhibits orienting of covert attention, of gaze direction and, more generally, of spatial responses toward tagged locations and objects. The presentation in this review of IOR, from its discovery by Posner and Cohen in 1984 to the present day, is perhaps more integrated than might be intuited from an exhaustive survey of studies that lay claim to the term. (p. 145)

He pointed to a variety of nonspatial, seemingly inhibitory phenomena that researchers either assimilated into the concept of IOR or distinguished from it. Klein concluded,

As our knowledge of the characteristics of IOR and its neural implementation grows, there will hopefully be increasing agreement on the use of the term. In the meantime, it is important to be careful but open-minded when choosing terms to divide up the psychological–biological realm. (p. 145)

Habituation is one of the most ubiquitous properties of the nervous system of organisms. My goal in the present article has been to remind the field that orienting—just like any other response of the nervous system—is subject to habituation, and to suggest that the neural mechanism underlying much of what we have come to call IOR can be fruitfully reconceptualized as habituation of spatial orienting. One benefit of this reconceptualization is that it provides a conceptual basis for “dividing up the psychological–biological realm.” General characteristics of the orienting reflex share with IOR that there is habituation, but the orienting reflex is distinguished from IOR in that the pathways being habituated are not necessarily spatial. Conversely, some putatively inhibitory spatial aftereffects of stimulation may have more to do with memory retrieval than with habituation and thus would be distinguished from IOR on this basis. Another benefit derives from the closer relation between brain and behavior, and, consequently, between neurophysiologists and psychologists, that is entailed in viewing IOR as habituation of spatial orienting. Finally, because each field has really looked at this effect in very different ways, there is an opportunity for both fields to gain insights into orienting and attention that may have, up until this point, been considered completely unrelated.

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to K. R. Dukewich, Psychology Department, Dalhousie University, Halifax, Nova Scotia B3H 4J1 Canada (e-mail: dukewich@dal.ca).

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NOTES

1. There have been some inconsistencies in observing this particular characteristic in the habituation literature (see Barry, 2006, for a more complete discussion of the issues).
2. This is true even in tasks that require participants to discriminate the target, because although the voluntary response is to identify the target, the reflexive spatial orienting response is a prerequisite for processing it.
3. It should be pointed out that neurophysiologists might argue that cross-modal IOR could, in fact, be accounted for by adaptation of neurons in areas of the brain that process space multimodally, such as in the deep layers of the SC (Meredith & Stein, 1983), as well as in parts of the parietal cortex (Avillac, Olivier, Denève, Hamed, & Duhamel, 2004).
4. The one exception was the most recently cued location, which continued to show a significant IOR effect. This could be the effect of sensory adaptation, or, as Snyder and Kingstone (2001) suggested, it may be due to either motoric effects of repetition or some reflexive orienting that cannot be completely inhibited by participants.
5. Although multiple sequential colors have not specifically been studied, this sort of effect was found by Lovibond (1969) using multiple sequential stimuli. Lovibond presented participants with a light that could be followed by a tone. Habituation was greatest when the light was always presented alone or when the tone was always presented following the light; however, no matter what the ratio of light:tone presentation, the galvanic skin response was decremental over stimulus presentations as compared with the first presentation of the light. Although this example is between-modalities, it is reasonable for one to assume that a similar effect can occur within a modality for different stimuli. See also del Rosal, Alonso, Moreno, Vázquez, and Santacreu (2006) for a computation model for habituation of simple and multiple stimuli.
6. The only exception was in the one-cue condition. In all other conditions, the rate of presentation was established within a trial with the presentation of more than one cue; however, this was not possible in the one-cue condition, so participants could not derive the time interval between the cue and the target in this condition. In all other conditions, the presentation of the target was temporally predictable on the basis of the rate of presentation established by multiple cue presentations.
7. It should be noted that these are conservative estimates made on the basis of the methods and the average RTs reported by Maylor and Hockey (1985).

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