Chapter 7

A Neurophysiological Correlate and Model of Reflexive Spatial Attention

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The importance of the distinction between reflexive and voluntary orienting is often overlooked, despite the fact that much research has documented differences in behaviour, physiology, and anatomical structure that are critically involved in reflexive (passive, bottom-up) and voluntary (active, top-down) saccades (Briand et al. 1999; Klein et al., 1992; Munoz, 2002; Pierrot-Deseilligny et al., 1991; Sereno and Amador, 2006; Sereno and Holzman, 1996). With respect to covert orienting, or spatially selective attention, both a non-predictive peripheral cue and a centrally presented, predictive, symbolic cue will result, for a certain interval of time, in subjects being able to better detect, identify, and discriminate stimuli at the cued location. The peripheral cue reflexively draws attention, whereas the central cue causes a voluntary shift of attention. Much research has also shown that reflexive and voluntary attentional shifts differ in behaviour, including time-course and valence (facilitation versus inhibition), physiology, and brain structures (Corbetta et al., 1993; Rafal et al., 1989; Rosen et al., 1999; Sereno et al., 2006b). In this chapter, we focus on understanding and providing a neurophysiologically plausible mechanism of reflexive spatial attention. We will argue that the neurophysiological expression of inhibition of return (IOR) in the superior colliculus (SC) bears resemblance to repetition suppression effects previously reported in ventral cortical areas and, most recently, a dorsal stream cortical area, the lateral intraparietal cortex (LIP). With a simple model of neurons that show an adaptive response, we demonstrate that the output of the network mimics the behavioural attentional findings that result after the onset of a non-predictive reflexive cue: namely, facilitation in responding to the target at short cue-target intervals and IOR at longer cue–target intervals. Given that many neurons in both LIP and ventral stream cortical areas have been shown to be shape selective, the model makes a further prediction that the shape of the cue will influence

spatial attention. In particular, it predicts that a cue with the same shape as the target will suppress spatial attention, due to shape specific adaptation effects. Preliminary behavioural data from our own lab, as well as previously published data from different paradigms support this contention. In sum, we demonstrate that a neurophysiologically plausible model, whose neurons incorporate a simple adaptive mechanism, results in output that mimics the behavioural findings of reflexive attention, including both spatial and shape effects of the cue on the response to a subsequent target.

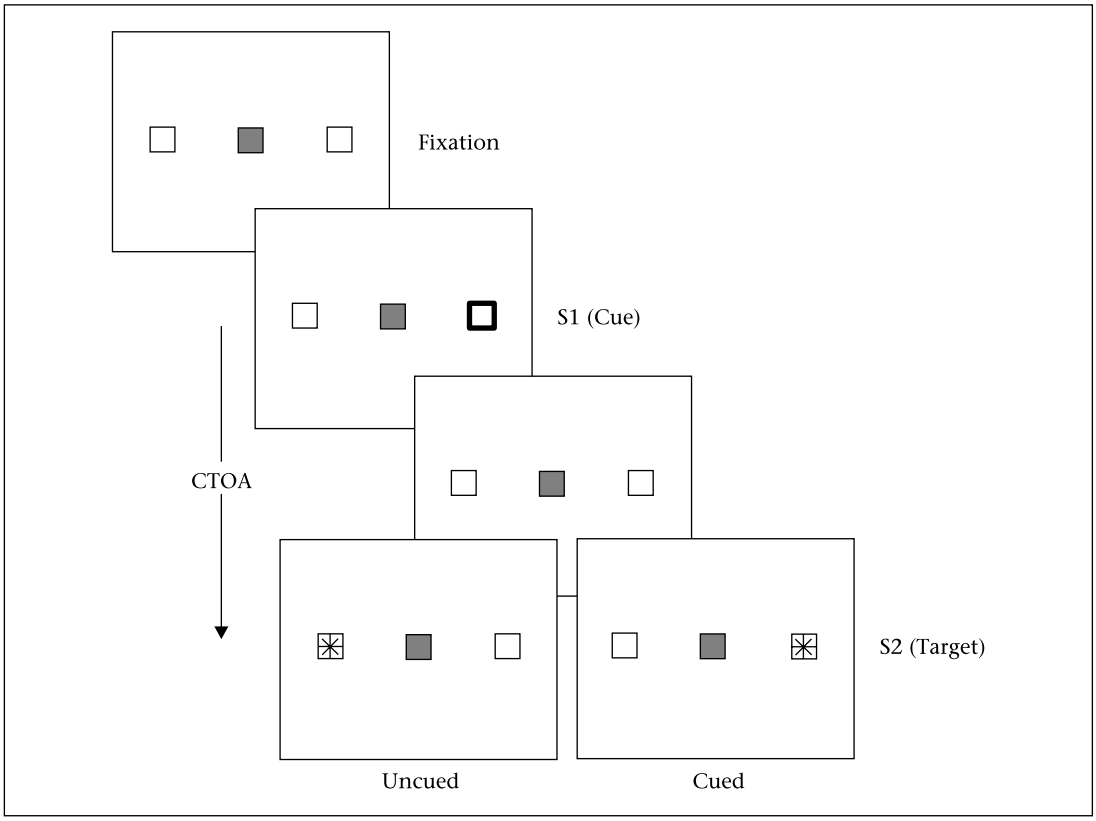
The consequence of these findings for understanding reflexive spatial attention is briefly discussed: *(a)* A simple adaptive mechanism, similar to what has been previously described as repetition suppression, is sufficient to explain reflexive attentional effects, including both spatial and shape effects; *(b)* This adaptive mechanism has been demonstrated in the superior colliculus, LIP, and ventral stream areas and hence may be a property of many brain regions, suggesting that reflexive attentional effects are a ubiquitous and distributed property of the brain; *(c)* Given that different brain regions manifest different properties and selectivities, the adaptive effects are specific and dependent on the stimulus properties and organization of stimulus properties represented in each area. Thus, as we have demonstrated for shape (Patel et al., 2007), we propose that spatial attentional effects may appear in many forms; and finally, *(d)* Although some have proposed that the facilitation and inhibitory (IOR) effects due to reflexive attention may be independent effects that occur simultaneously, we show that both can be explained by a single adaptive mechanism. We also demonstrate that this single mechanism can account for the modulation of attentional effects that are dependent on the shapes of the cue and target. Thus, although we do not preclude independent facilitatory and inhibitory effects, we show that separate mechanisms are not a necessary requirement.

INHIBITION OF RETURN (IOR)

Behaviour

Much research has focused on the behavioural effects that occur in a reflexive spatial attention paradigm (for review, see Egeth and Yantis, 1997; Klein, 2000; Wright and Ward, 1998). A typical spatial attention task that elicits IOR is illustrated in Figure 7.1. When a stimulus, S1, is flashed in the visual field, there are two well documented behavioural phenomena that follow. First, within approximately 50 to 150 ms, the response to a second stimulus, S2, that appears in the same location as S1 (cued trial, Figure 7.1) compared to other locations of the visual field (uncued trial, Figure 7.1) is facilitated (green section, Figure 7.2). This reflexive spatial attentional facilitation has been documented for a variety of responses, including detection, localization, and discrimination of non-spatial features, and has been observed for both manual and saccadic responses (see Sereno et al., 2006a for a review).

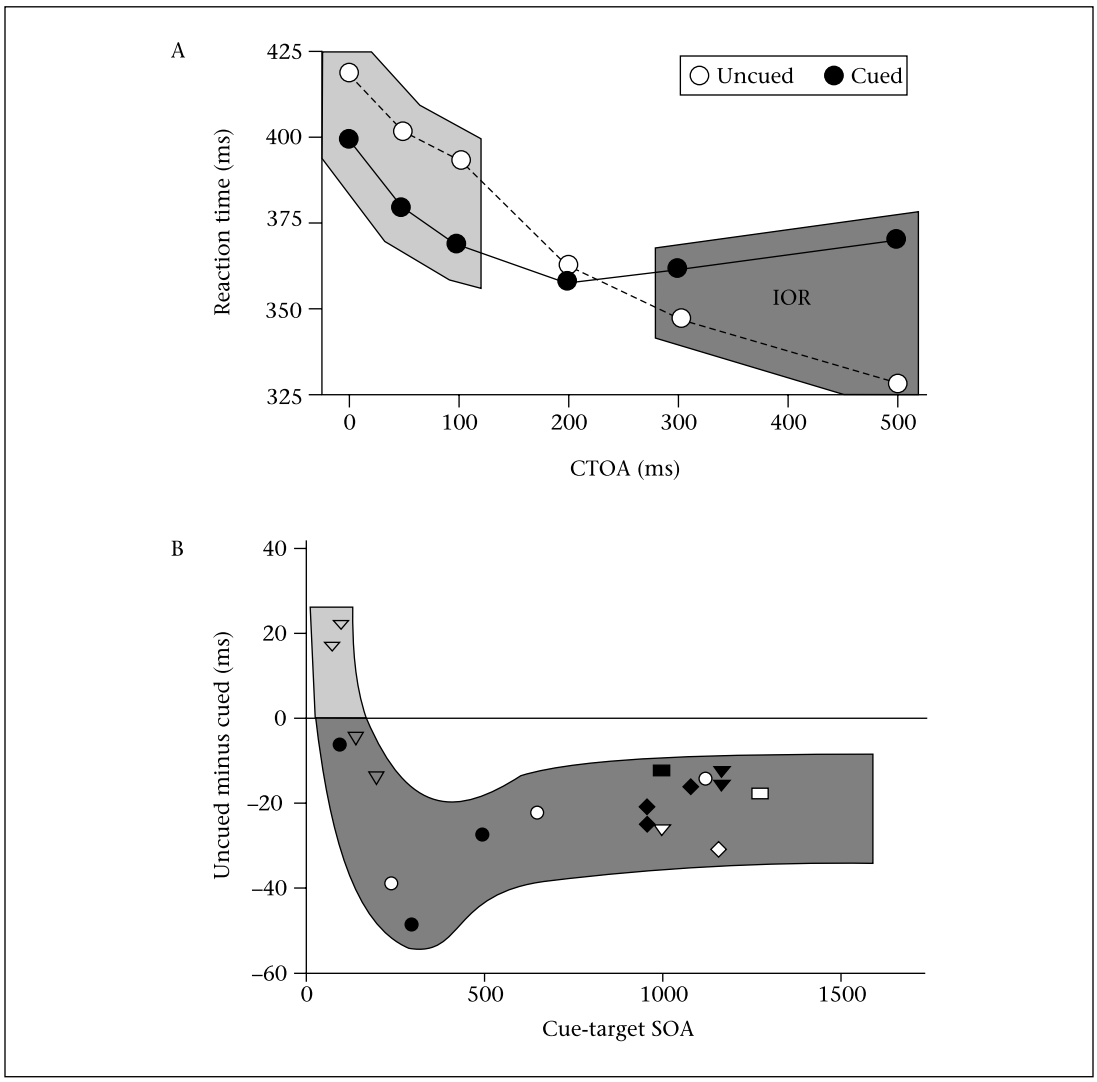
FIGURE 7.1 Typical reflexive spatial attention task used to elicit IOR



Note: After the subject fixates, one of two boxes brightens (S1 or cue). Following a variable interval of time (CTOA), a second stimulus (S2 or target) appears and the subject responds as quickly as possible. The figure shows two possible target conditions. An uncued trial, where S2 appears in a location other than the location of S1. A cued trial, where S2 appears in the same location as S1. Figure adapted from Klein, 2000.

Second, the facilitation effect is followed at cue–target onset asynchronies (CTOAs) of 150 ms or more by an opposite, inhibitory effect; hence the name, inhibition of return (see red section, Figure 7.2). IOR was first described by Posner (1980) and Posner and Cohen (1984). IOR has also been reported for a variety of classification responses and response modes (see Klein, 2000, for a review; but see also Khatoon et al., 2002). The standard interpretation of these behavioural findings is that a peripheral visual event automatically draws attention to the position of the stimulus. This initial reflexive shift of attention toward the source of stimulation results in facilitation of the processing of all nearby stimuli. However, when the event is not task-relevant, attention shifts away and

FIGURE 7.2 Typical behavioural results obtained in a reflexive spatial attention task



Note: (A) With short cue-target onset asynchronies (CTOAs), subjects are faster to respond on cued trials, when S2 appears in the same location as S1. At longer CTOAs, subjects are faster to respond on uncued trials, when S2 appears in any location other than S1. Data from a task with manual response. (B) The time course of attentional effects in saccade paradigms. Data combined from 8 studies. Data plotted as differences in saccadic reaction times (uncued minus cued) as a function of CTOAs. The period of reflexive spatial attentional facilitation is highlighted in green. The period of reflexive spatial attentional inhibition is highlighted in red and referred to as inhibition of return (IOR).

Source: Figures adapted from Klein, 2000.

there is an inhibition of attentional resources returning to previously attended locations. This inhibitory effect is measured as a delayed response to stimuli subsequently displayed at the originally cued location. Whether the slowing of response is due to inhibition of sensory analyses or to inhibition of motor response to previously cued locations remains debatable (Fecteau and Munoz, 2007; Sereno et al., 2006a; Taylor and Klein, 2000).

Anatomical Localization

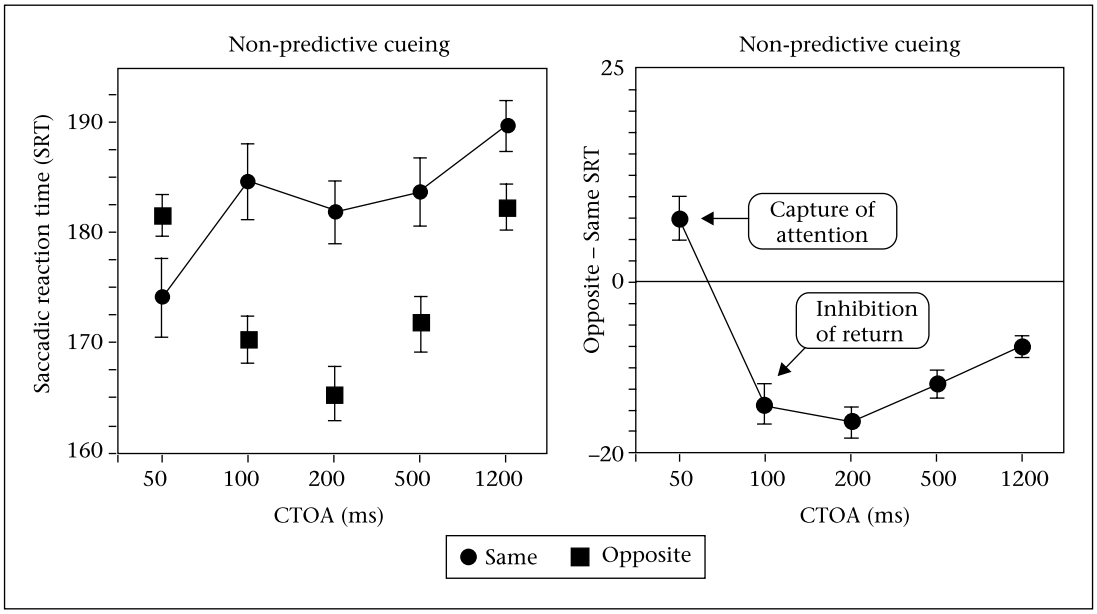
Several lines of evidence have suggested that the SC is involved in the generation of IOR (for review, see Sereno et al., 2006b). Much of this evidence comes from behavioural studies in humans. The first evidence supportive of collicular involvement in IOR came from studies performed in patients with progressive supranuclear palsy. A common early symptom is disruption of eye movements. This deficit is thought to be caused by degeneration in the SC and adjacent midbrain structures. In a series of studies, Posner, Rafal, and colleagues demonstrated that progressive supranuclear palsy patients showed deficits in early facilitation and later IOR (Posner et al., 1982; Posner et al., 1985; Rafal et al., 1988).

Other behavioural evidence suggesting that the SC is involved in IOR comes from reports of differences in orienting effects between the temporal and nasal visual fields. The visual pathways leading into the SC include a greater representation of the contralateral nasal hemiretina (temporal visual field) than the ipsilateral temporal hemiretina (nasal visual field). In 1989, Rafal and colleagues demonstrated that subjects performing a spatial attention task monocularly showed larger IOR effects in the temporal versus the nasal hemifield, corresponding to the greater representation of the temporal hemifield in retinotectal projections. Finally, two reports have demonstrated that patients with lesions of the SC fail to show IOR (Sapir et al., 1999; Sereno et al., 2006b). Until recently, no direct neurophysiological evidence has been produced in support of localization of IOR in the SC.

Physiology

A series of recent studies (Bell et al., 2004; Dorris et al., 2002; Fecteau et al., 2004) has examined the responses of single neurons in the SC of monkeys performing a spatial attention task in search of neural correlates of reflexive spatial attention effects. Like humans, monkeys show behavioural facilitation on cued trials (see Figure 7.3, blue line) compared to uncued trials (Figure 7.3, red line) at a short CTOA, and inhibition for cued trials at longer CTOAs (also see Figure 7.4A, top panel). These studies have identified neural correlates of both early facilitation and later IOR effects in the intermediate layers of the SC. At short CTOA intervals that result in behavioural facilitation of response for cued trials, there is relatively stronger target-related activity when the cue and target appear

FIGURE 7.3 Behavioural results of monkeys in a reflexive spatial attention task

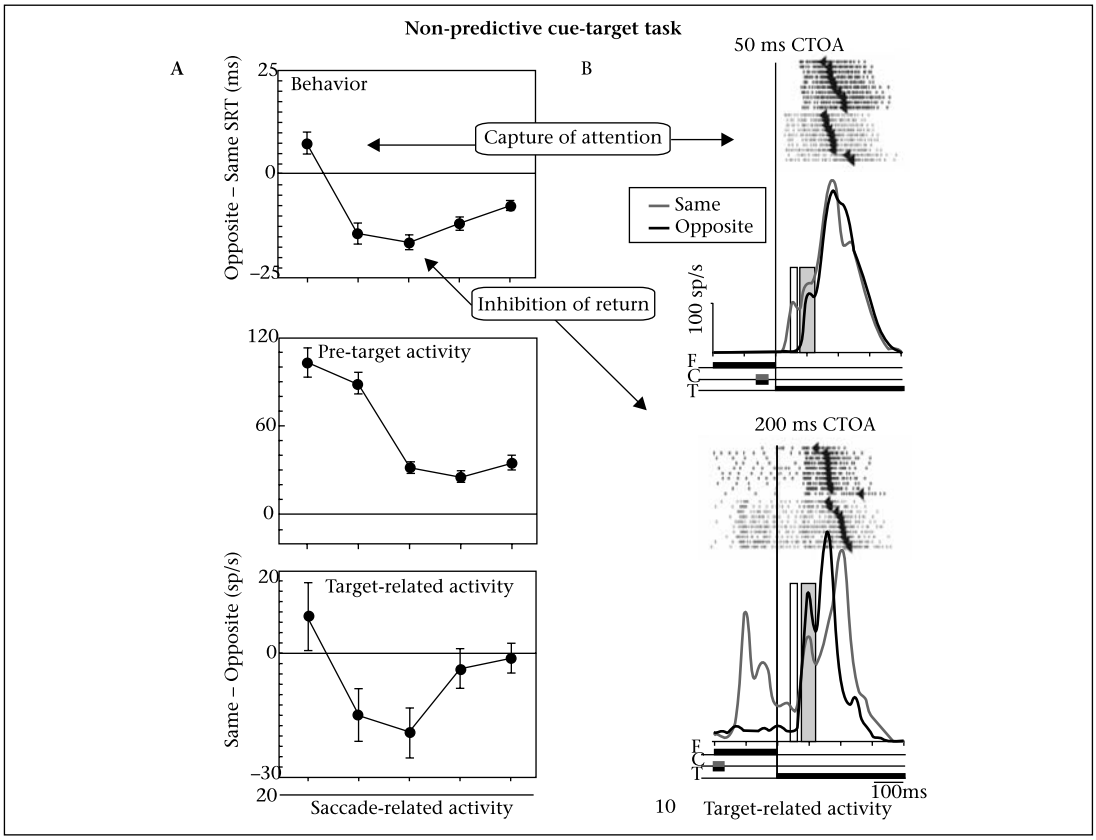


Note: The top panel shows that monkeys show a similar pattern to humans. Response times of cued trials when S2 (target) appears on the same side as S1 (cue) are shown in blue. Response times of uncued trials, when S2 appears on the opposite side as S1, are shown in red. These results show that monkeys also show facilitation on cued trials (blue line compared to red line) at the shortest CTOA, and inhibition on cued trials at the longer CTOAs (blue line compared to red line). The bottom panel displays the same data as differences between mean uncued (opposite) and cued (same) conditions, again showing facilitation at the shortest CTOA and inhibition at greater CTOAs.

Source: Figure adapted from Fecteau et al., 2004.

at the same location versus different locations (Bell et al., 2004; Fecteau et al., 2004). In particular, Figure 7.4B (top panel) demonstrates that the response of an example neuron to the target, indicated by the gray region, is greater on cued trials (blue line) than on uncued trials (red line). At longer CTOA intervals that result in behavioural inhibition of response for cued trials, these studies further show that there is relatively weaker target-related activity when the cue and target appear at the same location compared to different locations. Figure 7.4B (bottom panel) demonstrates that the response of this neuron to the target, indicated by the gray region, is suppressed on cued trials (blue line) compared to uncued trials (red line). Dorris et al. (2002) showed that the magnitude of this suppressed response was correlated with subsequent slowing in saccadic reaction times. This attenuation of activity during IOR is direct evidence that the SC is involved in the manifestation of IOR.

FIGURE 7.4 Activity of SC neurons during a reflexive spatial attention task



Note: (A) Population averages for saccadic response times (top panel, same as bottom panel of Figure 3 showing the 5 CTOAs), pre-target-related activity (middle panel), and target-related activity (bottom panel). Pre-target activity (middle panel) shows maintained activity on cued trials at long CTOAs. Target-related activity (bottom panel) shows that population activity of cued trials compared to uncued trials are greater at the shortest CTOA, but suppressed at CTOAs of 100 and 200. (B) Neural activity of two representative SC neurons. Top panel shows the averaged activity of a neuron at the 50 ms CTOA when S1 and S2 appeared in the response field (blue line, cued trials) or just S2 appeared in the response field (red line, uncued trials) of the neuron. At the 50 ms CTOA, the behavioural response of the monkey to the target is facilitated on cued trials. Note that the neural response to the target (period highlighted in gray) is greater on cued trials (blue) compared to uncued (red) trials. Bottom panel shows the averaged activity of a second neuron at the 200 ms CTOA when S1 and S2 appeared in the response field (blue line, cued trials) or when just S2 appeared in the response field (red line, uncued trials) of the neuron. At the 200 ms CTOA, the behavioural response of the monkey to the target is inhibited on cued trials. Note that the neural response to the target (period highlighted in gray) is reduced on cued trials (blue) compared to uncued (red) trials. In addition, the bottom panel illustrates that during the pre-target period (white box immediately preceding the gray target period) that there is maintained activity on cued trials (blue) compared to uncued trials (red). Figure adapted from Fecteau et al., 2004.

Dorris et al. (2002), however, also argued that SC is not the site of inhibition because the observed attenuation of activity during IOR was not caused by active inhibition of those neurons which were, in fact, more active following the presentation of the first stimulus (cue, S1) in their response field. As shown in Figure 7.4B (bottom panel), the activity of the neuron after the presentation of S1 (cue), but before the presentation of S2 (target), is greater than baseline activity. That is, in the period of time immediately preceding the presentation of S2 (period marked by white box, immediately preceding target period marked in gray), the activity of neurons in SC is greater on cued trials (blue line) than on uncued trials (red line). When they repeated the same experiment and induced saccades by electrical microstimulation of the SC in order to assess the level of excitability of the SC circuitry during the IOR task, they found that faster saccades were elicited from the cued location than the uncued location. Thus, they concluded that in monkeys, the SC participates in the expression of IOR but is not the site of the inhibition. In particular, they suggested that reduced activity in the SC reflects a signal reduction that has taken place upstream, perhaps in posterior parietal cortex.

This greater activity in the S1–S2 (cue–target interval) was perplexing because prior studies of motor preparation (for example, Dorris and Munoz, 1998; Dorris et al., 1997) had shown that similar increases in pre-target activity were associated with shorter, not longer, saccade reaction times. Nevertheless, this physiological pattern of suppression for a repeated stimulus and maintained activity between stimulus presentations has been reported before in physiological studies of cortical areas, primarily from recordings in temporal, but not parietal, cortical areas. We briefly review this literature in the next section.

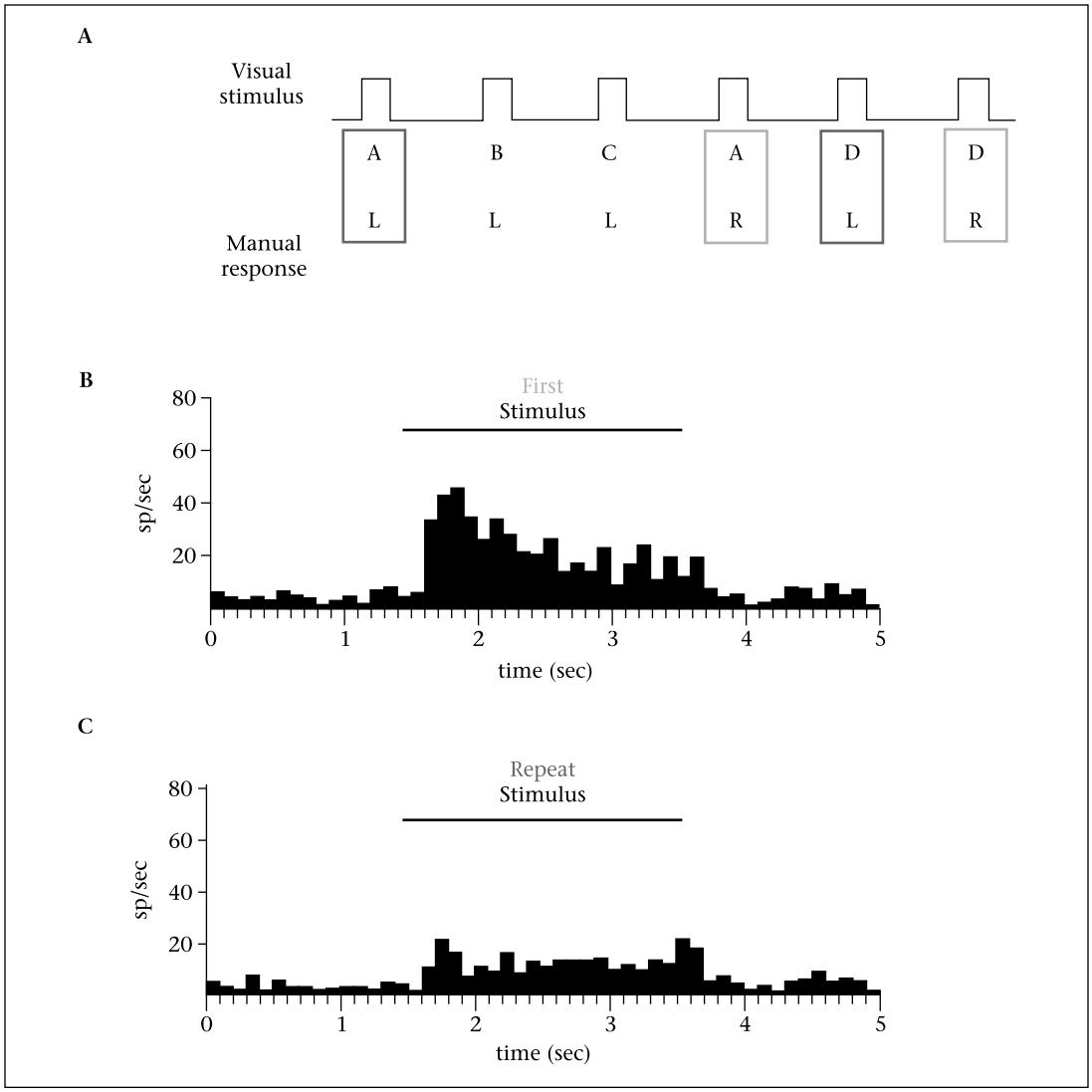
REPETITION SUPPRESSION

Ventral Stream Physiology

Visual sensory information proceeds through several cortical areas before it reaches inferotemporal cortex (Felleman and Van Essen, 1991). Neurons in inferotemporal cortex are sensitive to complex visual properties such as colour, shape, and facial structure (for reviews, see Logothetis and Sheinberg, 1996; Tanaka, 1996). Previous neurophysiological studies have also demonstrated that many neurons in inferotemporal cortex show a reduced response to a repeated stimulus.

The reduction in neuronal response to a repeated stimulus has been variously described or labeled: decremental response (Brown et al., 1987; Fahy et al., 1993); adaptive filtering (Desimone, 1992); stimulus specific adaptation (Ringo, 1996); or response suppression (Desimone, 1996); see Brown and Xiang (1998) for review. These effects have been reported from a number of different laboratories (Brown et al., 1987; Miller et al., 1993; Sobotka and Ringo, 1993) from recordings in various regions of inferotemporal cortex, including area TE, perirhinal cortex, and entorhinal cortex (Fahy et al., 1993). Figure 7.5

FIGURE 7.5 Stimulus repetition suppression effects in the ventral steam during a serial recognition task



Note: (A) Schematic representation of the task. The monkey was presented with different unfamiliar objects and pictures (indicated by the letters A, B, C, and D) and taught that the correct response was a left reach (L) to the first presentation and a right reach (R) to a subsequent presentation of a stimulus. The first (blue box) and repeated (red box) presentations of stimulus A and D are highlighted with boxes. (B) Histograms of a representative perirhinal neuron with activity averaged either across the first (left) or repeat (right) presentations of ten different unfamiliar stimuli.

Source: Figure adapted from Fahy et al, 1993.

illustrates a cell in perirhinal cortex that demonstrates a repetition suppression effect. The average response of the cell to 10 different stimuli is shown for the first (Figure 7.5B) and a repeated presentation (Figure 7.5C). Repetition suppression effects are also evident in population measures. Figure 7.6 illustrates average responses across a population of cells recorded in anterior inferotemporal cortex (AIT) while the animal performed one of two tasks (see Figure 7.6A). Figure 7.6B demonstrates that whether or not a repeated stimulus was a match (in a standard delayed match to sample task; dark yellow bars) or a nonmatch (in a delayed match to sample task with intervening nonmatch repeats; dark gray bars), there was a reduced response to the repeated stimulus compared to its first presentation in a trial (sample, light yellow bar; and nonmatch, light gray bars).

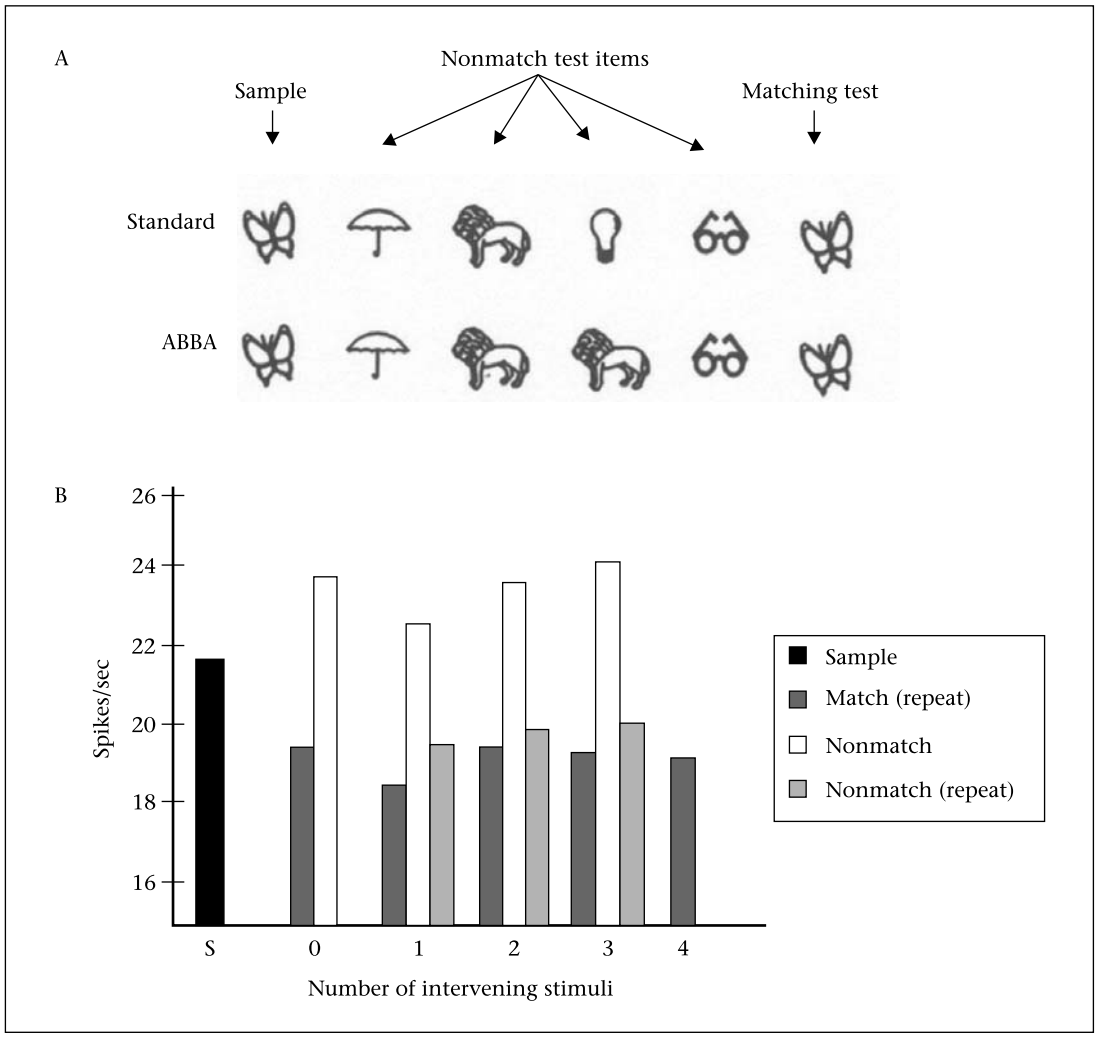
Interestingly, a repeated visual stimulus also elicits a reduced neural response in functional magnetic resonance imaging (fMRI). This decrease in blood oxygenation level-dependent (BOLD) response has been variously labeled fMRI-adaptation, repetition attenuation, or repetition suppression (Grill-Spector et al., 2006; Henson, 2003; Schacter and Buckner, 1998; Wiggs and Martin, 1998; Xu et al., 2007). In the last decade, this repetition suppression effect has been used in fMRI studies to measure neuronal selectivity in different regions of ventral visual cortex (for example, Epstein et al., 2003; Grill-Spector et al., 1999; Kourtzi and Kanwisher, 2001).

Lateral Intraparietal Cortex (LIP)

Too little research has explored stimulus specific repetition suppression effects in the dorsal stream visual areas. In part, this may be due to the widely held presumption that the ventral stream is important for object properties whereas the dorsal stream is important for spatial processing (Ungerleider and Mishkin, 1982; see also Figure 7.7). However, recent reports in the monkey (Sereno and Amador, 2006; Sereno and Maunsell, 1998; M. E. Sereno et al., 2002) demonstrate that shape information is present in neurons at a high level area of the dorsal stream, the lateral intraparietal cortex (LIP). In a comparison of shape encoding between dorsal and ventral visual pathways, Lehky and Sereno (2007) demonstrate that stimulus repetition of a 2D geometric shape in a passive fixation task (Figure 7.8) causes a response decrement in both AIT and LIP. This repetition suppression effect is apparent in plots of the peristimulus responses (Figure 7.9) averaged over all shape stimuli and all shape selective cells in AIT (red lines) and LIP (blue lines). As illustrated in Figure 7.9, averaged population responses of neurons in AIT and LIP are greater in the first presentation of a stimulus in a trial (solid coloured lines) compared to subsequent stimulus repetitions within a trial (dashed lines). These findings document the first report of shape selective repetition suppression effects in LIP (see arrow labeled RS in Figure 7.9).

Figure 7.9 also shows that neurons in LIP have significantly higher average firing rates to the various shapes than do neurons in AIT. After normalization, however, Lehky and Sereno, (2007) demonstrated that repetition suppression effects were not significantly

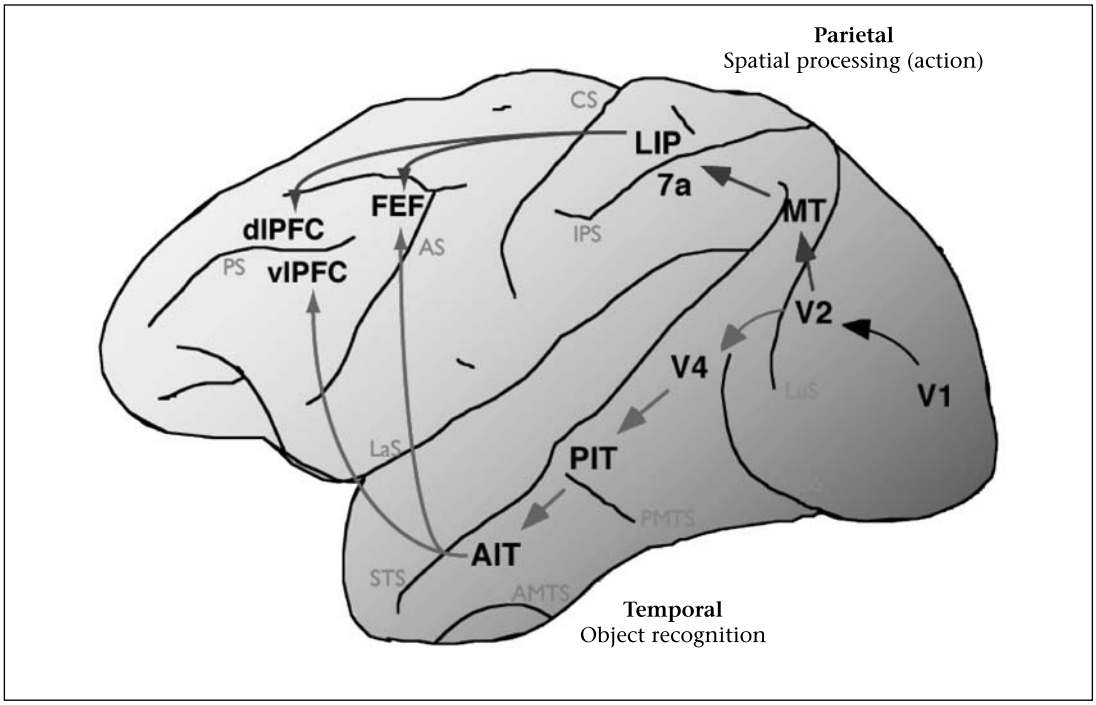
FIGURE 7.6 Stimulus repetition suppression effects in the ventral steam during delayed match-to-sample tasks



Note: (A) Schematic representation of the tasks. The monkey was trained to initiate a trial by holding down a lever. After fixating a small fixation target, up to 5 different familiar objects and pictures were presented (e.g., butterfly, umbrella). The first stimulus of the trial was the sample and the animal was trained to release the lever when the same stimulus (match) was presented again. In the standard task, the intervening nonmatch stimuli were never repeated. In the ABBA design, interleaving nonmatch stimuli could also repeat. (B) Average activity across neurons with a significant repetition suppression effect in inferotemporal cortex. Panel B illustrates that repeated presentation of a stimulus, whether a match (dark yellow) or repeated nonmatch (dark gray) was reduced compared to the first presentation of the stimulus in a trial, either as the sample (light yellow) or the first presentation of a nonmatch (light gray).

Source: Figure adapted from (Miller and Desimone, 1994).

FIGURE 7.7 Schematic localization of visual pathways in the macaque brain

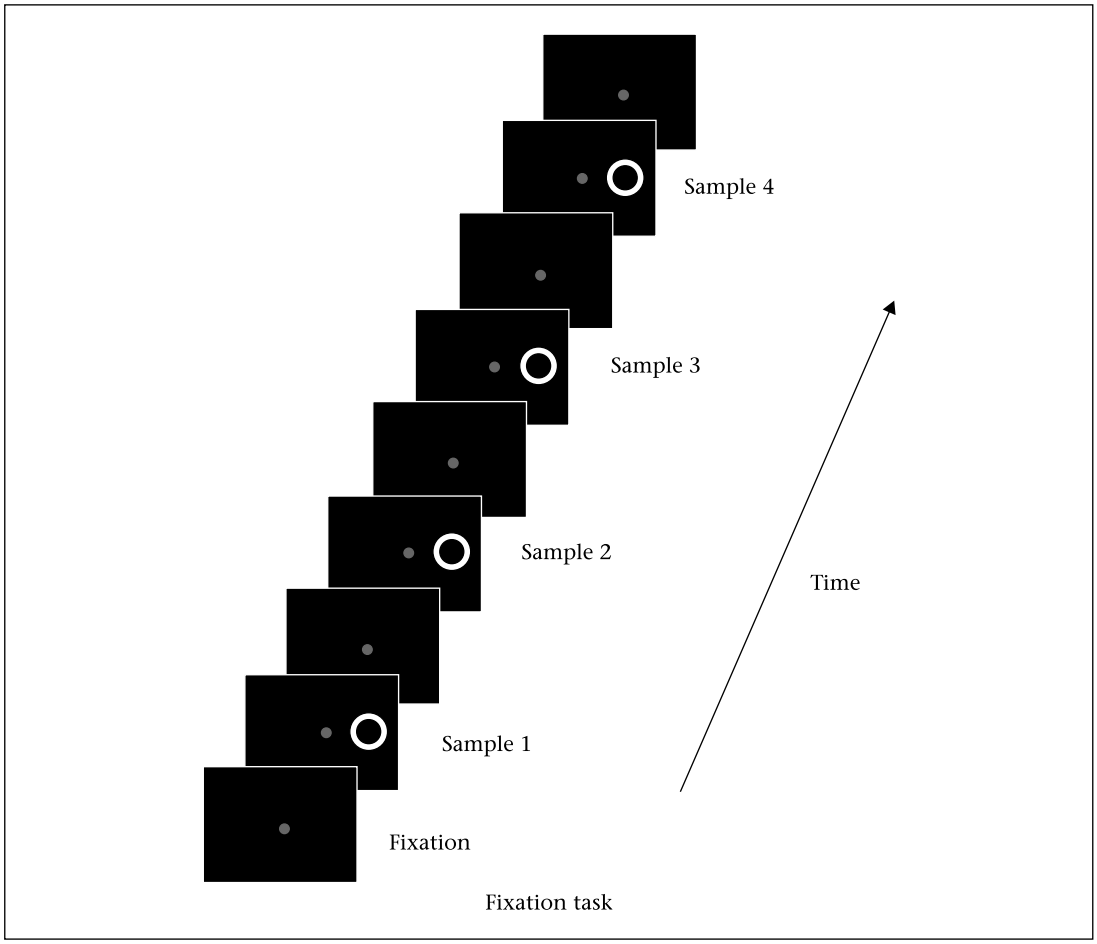


Note: This indicates a major visual areas along the dorsal pathway (blue arrows) and ventral pathway (red arrows). The lateral intraparietal area (LIP), located on the lateral bank within the intraparietal sulcus (IPS), is a high-level area in the dorsal pathway. Anterior inferotemporal cortex (AIT), including the lower bank of the superior temporal sulcus (STS) and convexity of the middle temporal gyrus, is a high-level visual area in the ventral pathway. The frontal eye field (FEF), including cortex in the rostral bank of the arcuate sulcus (AS), receives projections from both LIP and AIT. Dorsolateral prefrontal cortex (dlPFC), including the cortex of the principal sulcus (PS) and dorsal to the PS, and ventrolateral prefrontal cortex (vlPFC), including cortex ventral to the PS, are prefrontal cortical areas receiving heavy projections from LIP and AIT, respectively. (LuS: Lunate sulcus; LaS: Lateral sulcus; CS: central sulcus.)

Source: Adapted from Lehky and Sereno, 2007.

different for the two areas (see Figure 7.10). Miller et al. (1993) and Holscher and Rolls (2002) have argued that there is an active reset mechanism in AIT that restricts the repetition suppression effect to stimuli presented within a single trial such that suppression does not continue even in the short duration until the next trial. This suggests that repetition suppression is an active, task-related cognitive process, not simply a biophysical adaptation effect. In our data, repetition suppression effects in LIP neurons are consistent with reset between short blocks of trials (see Figure 7.11). However, the average time between presentation onsets within a trial in Figure 7.11 was approximately 900 ms whereas the

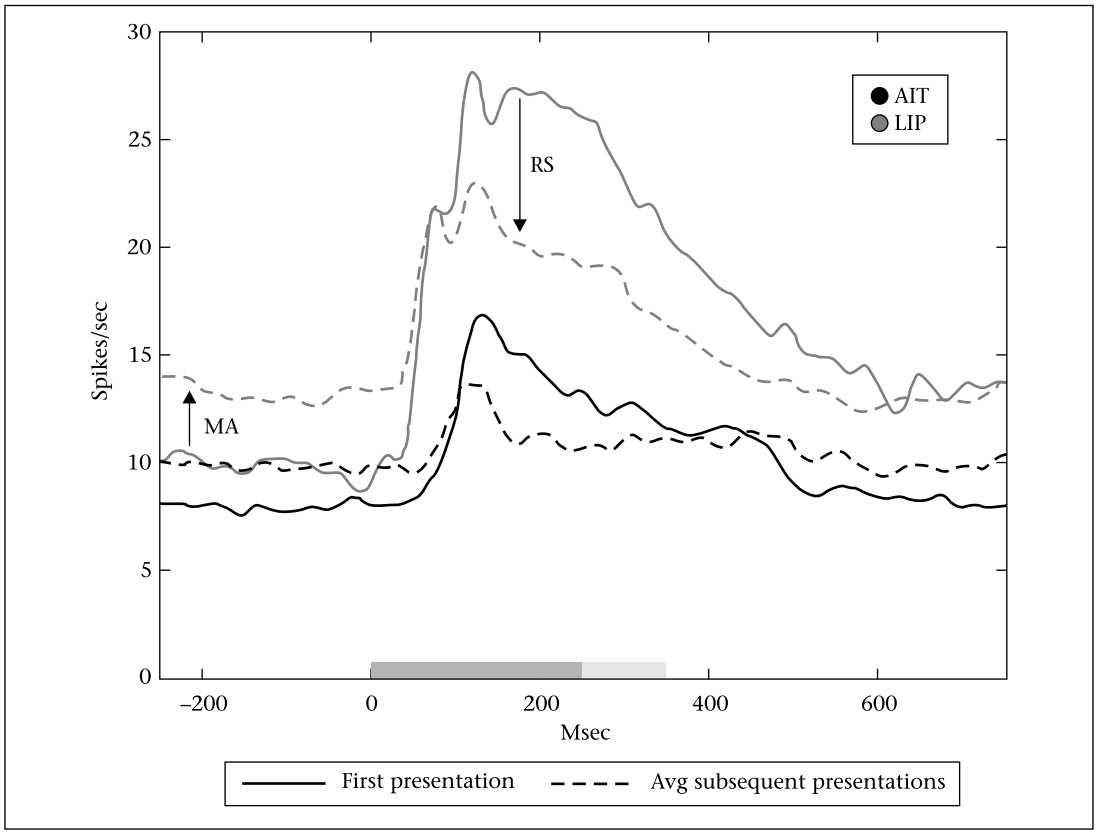
FIGURE 7.8 Schematic diagram of the fixation task (1 location, 8 shapes)



Note: The stimulus for each trial in the fixation task is selected from a set of eight different shapes. All shapes are centred on the same position within the cell's receptive field. For each trial, one randomly selected shape is presented for typically 4 repetitions before a central fixation spot is extinguished. Stimulus duration and the blank interval following each stimulus repetition are constant (typically 350 ms and 750 ms, respectively). The animal is required to maintain fixation within 0.5° of the central 0.1° spot in the centre of the video display throughout the trial. The animal is rewarded for maintaining fixation of the central spot until it disappears. A minimum of six trials is presented for each shape.

average time between presentations between blocks was minimally 21 sec (average of 4 trials). A relatively fast recovering adaptation function would appear to reset between trials. Hence, it remains for quantitative studies across different brain regions to determine whether repetition suppression is a function of time versus trial and task structure.

FIGURE 7.9 Activity of AIT and LIP shape selective neurons during a passive fixation task with repeated stimulus presentations within a trial



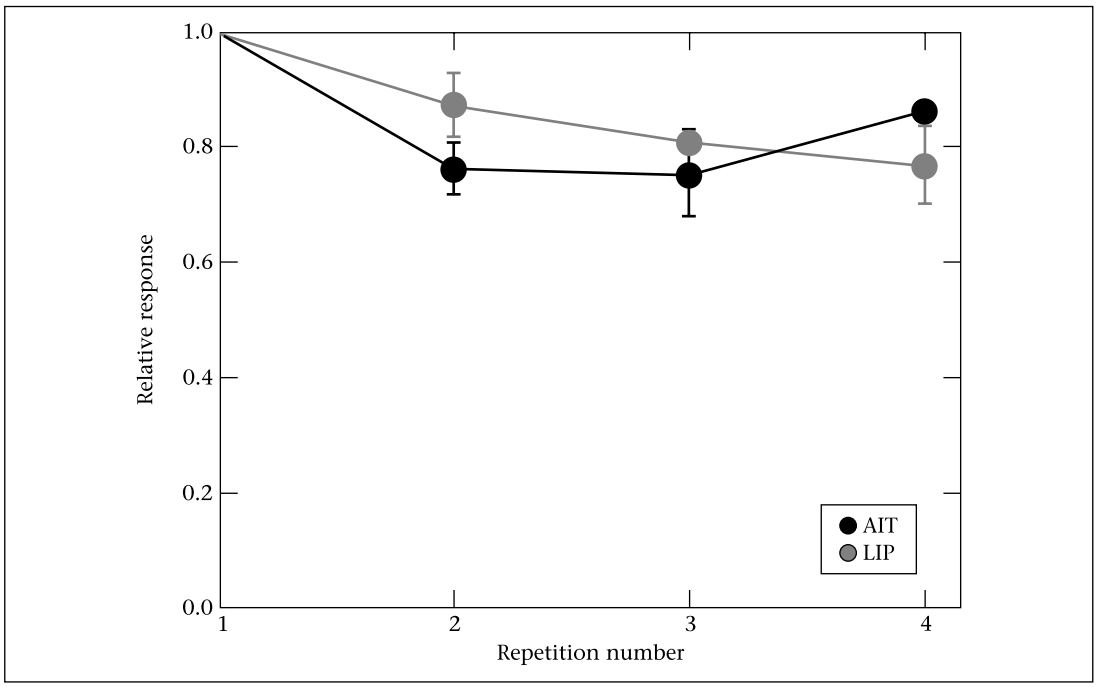
Note: Solid lines show responses to the first presentation, whereas dashed lines show average response over all subsequent stimulus repetitions within a trial. Green bar at bottom indicates stimulus presentation period, which varied between 250 (darker green) and 350 ms in different units. The arrow labeled (a) indicates repetition suppression effects in LIP. A similar reduction in response can be seen in AIT responses (red lines). Activity preceding the zero on the x-axis shows baseline activity (solid lines) or maintained activity between stimulus repetitions (dashed lines). The arrow labeled (b) indicates maintained activity in LIP. A similar increase in baseline response can be seen in AIT responses (red lines).

Source: Figure adapted from Lehky and Sereno, 2007.

Maintained Activity in AIT, LIP, and SC

Lehky and Sereno (2007) also called attention to another aspect of AIT and LIP responses that is apparent in Figure 7.9, namely, that the activity of neurons in both areas does not return to baseline between stimulus presentations within a trial. This maintained activity between presentations is most clearly seen on the left side of Figure 7.9 (see arrow labeled MA)

FIGURE 7.10 Repetition suppression effects in AIT and LIP



Note: In both cortical areas, repeat presentations of the same stimulus within a trial produced a decreased response relative to the first presentation. Responses for each cell have been normalized relative to the first stimulus presentation and then averaged together for each cortical area.

Source: Figure from Lehky and Sereno, 2007.

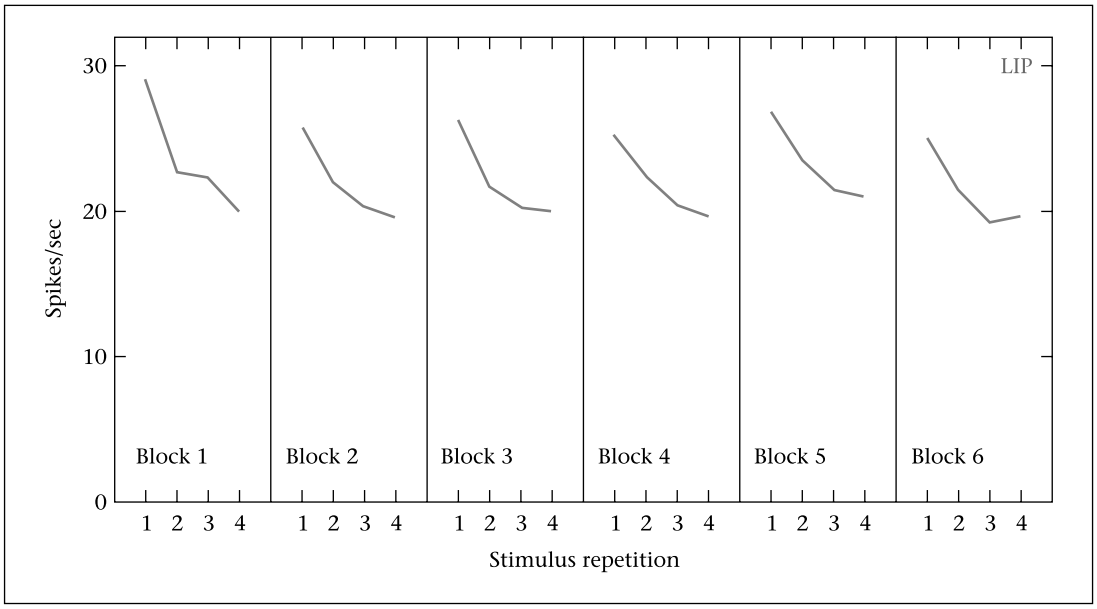
where the average baseline firing rate before subsequent presentations in a trial (dashed lines) is greater than the firing rate before the first presentation of the stimulus (solid lines). Interestingly, this maintained activity in AIT and LIP resembles the elevated baseline activity reported by Dorris et al. (2002) in the SC. As with repetition suppression effects, maintained activity may be a ubiquitous reflexive response property occurring in many areas of the brain.

MODEL OF REFLEXIVE SPATIAL ATTENTION

Repetition Suppression as a Manifestation of IOR

Recent neurophysiological studies in SC have shown that at longer CTOA intervals that result in IOR, there is relatively weaker target-related activity when cue and target appear at the same, compared to different, locations (Bell et al., 2004; Dorris et al., 2002;

FIGURE 7.11 Repetition suppression effects in LIP across 6 blocks of trials



Note: Repeat presentations of the same stimulus within a trial produced a decreased response relative to the first presentation, but the average activity largely recovered between blocks. Each block consisted of eight trials (one for each shape stimulus) presented in random order. Data were pooled over all neurons showing shape selectivity and included responses for all stimuli.

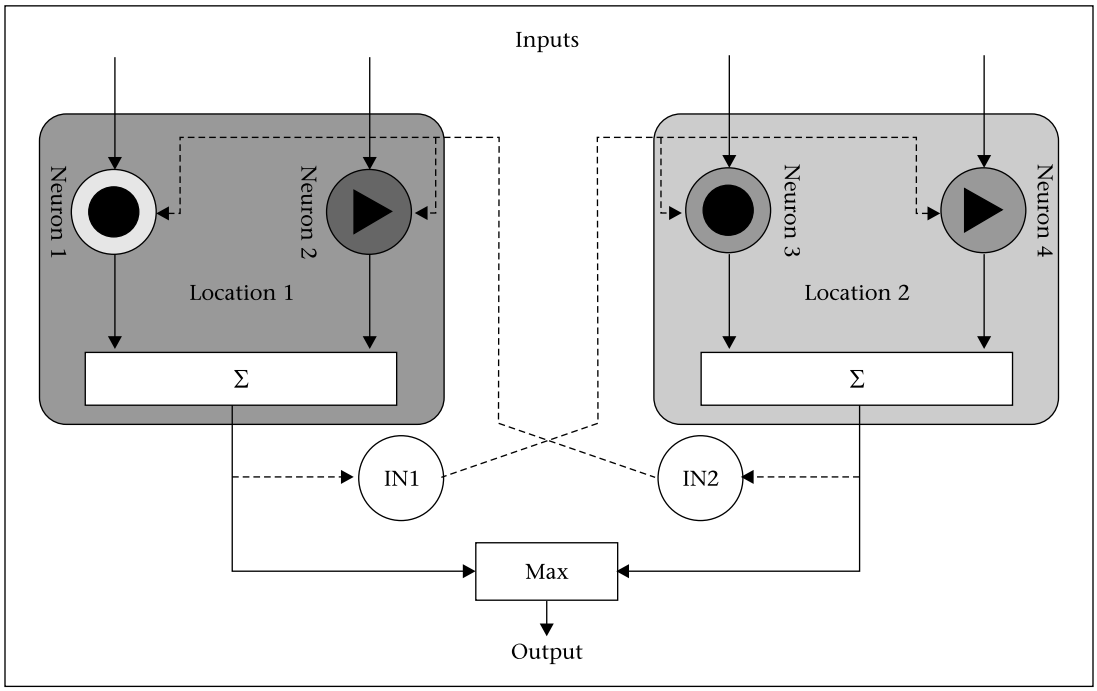
Fecteau et al., 2004). These changes in the neural representation of the target were tightly coupled with subsequent saccadic reaction times. This repetition suppression effect is direct evidence that the SC is involved in the manifestation of IOR.

A Model with Repetition Suppression as the Mechanism of Reflexive Spatial Attention

We hypothesize that behavioural reflexive spatial attentional effects can be explained by repetition suppression of neuronal responses. Given that different brain regions are selective for different stimulus properties, we suggest that suppression effects may be specific and dependent on the stimulus properties represented in each area. If repetition suppression effects in other cortical areas are related to the manifestation of reflexive attentional effects, as they are in the SC, there may be a form of reflexive spatial attention that is indeed sensitive to the shape of the cue and target. In many reflexive attention tasks, the cue has a different shape than the target (for example, see Figure 7.1). To model the effects of repetition suppression while allowing for shape selectivity, we created a small

network of four neurons (two shape selective neurons for each of two locations), each with an adaptive mechanism, mutually inhibitory spatial interactions, and non-linear dynamics (see Figure 7.12; Patel et al., 2007). In our model neuron, the adaptive mechanism is identical to those utilized in model neurons of retinal computations (Abbott et al., 1997; Grossberg, 1972; Ogmen, 1993). Such models are also employed in perceptual models of blur discrimination (Purushothaman et al., 2002) and visual masking (Ogmen et al., 2003). We compute the model's output by first summing the activity of the two shape selective neurons at each location. The model's output is the larger of the summed

FIGURE 7.12 Proposed network model of reflexive spatial attention

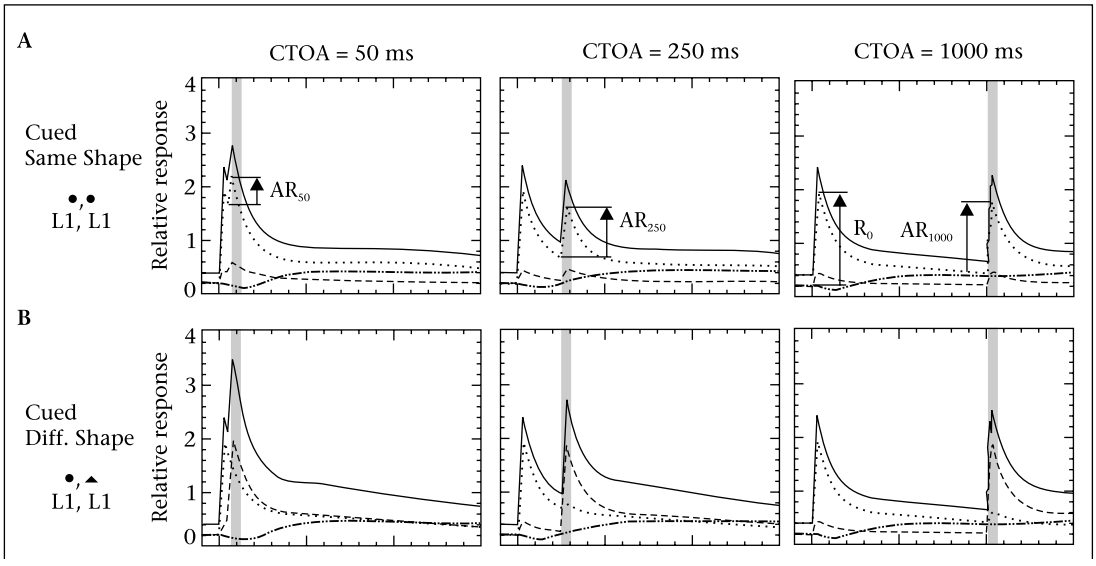


Note: This simple model consists of four neurons. The receptive fields of Neurons 1 and 2 represent Location 1, whereas the receptive fields of Neurons 3 and 4 represent Location 2. In addition, Neurons 1 and 3 prefer one shape (circle), and Neurons 2 and 4 prefer a second shape (triangle). Each neuron can be excited directly by visual stimuli (cue or target). Neurons from one location inhibit neurons representing other locations (dashed lines) via tonic interneurons (IN1 & IN2). For simplicity, this mutual inhibition is shown to originate after the outputs of all the neurons at one location are summed. The activity from all neurons representing a given location are summed (S) and the larger of the two sums (MAX) is designated as the output of the model. The output of the model is used as the modulatory component on the behavioural response. Greater model output facilitates behavioural response and weaker model output slows behavioural response. Similar to psychophysical studies, the attentional effects of the model are then computed by comparing behavioural responses in the uncued and cued conditions.

activities at the two locations. We did not explicitly model the MAX readout mechanism but have used a scheme that can be implemented by a competitive winner-take-all type neural network (for example, Lo and Wang, 2006). An alternative implementation in which the model's output is equal to the difference between the summed activities at the two locations, yielded qualitatively similar results.

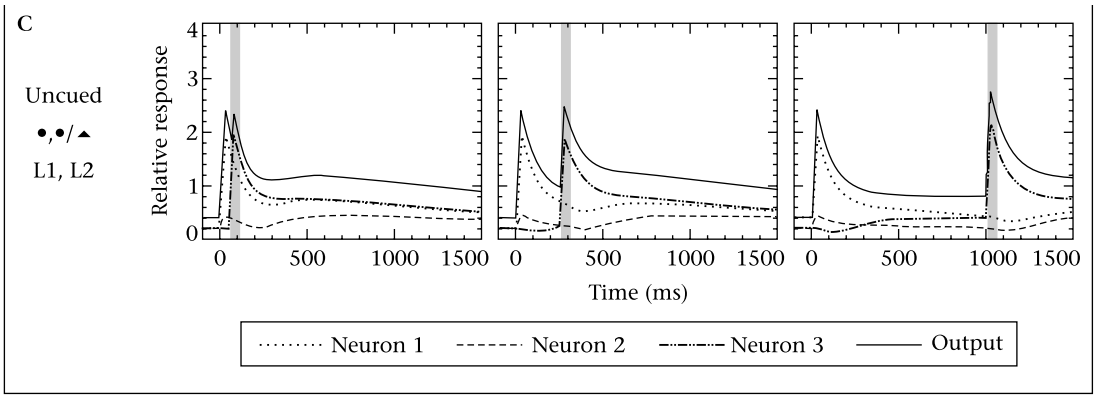
Figure 7.13 illustrates the response of individual neurons in the model (broken lines; colour coded to match neuron colour in Figure 7.12) and the output of the model (solid line) to the presentation of a cue (S1) and target (S2) under three different cueing conditions (rows) at three different CTOAs (columns). The first two rows (Figures 7.13A and 13B) represent two types of cued trials. The first row (Figure 7.13A) represents a cued trial in which the target has the same shape as the cue (target neuron response shown in light red), and the second row (Figure 7.13B), a cued trial in which the target has a different shape than the cue (target neuron response shown in dark red). The third row (Figure 7.13C) represents uncued trials in which the target appears in a different location than the cue (target neuron response shown in green). The period of time highlighted in gray in each of the nine graphs of Figure 7.13 represents the period over which the model's output is integrated to compute latency modulation of the behavioural response to the target. This period highlights each cell's activity associated with the target presentation (broken lines) as well as the output of the network (solid black line). The output of the model to the target in a particular cueing condition was used to compute the modulatory component of the response time (mRT) for that condition (higher output was associated with shortening

FIGURE 7.13 Simulated outputs of the model at three different CTOAs during a reflexive attention task



(*Continued*)

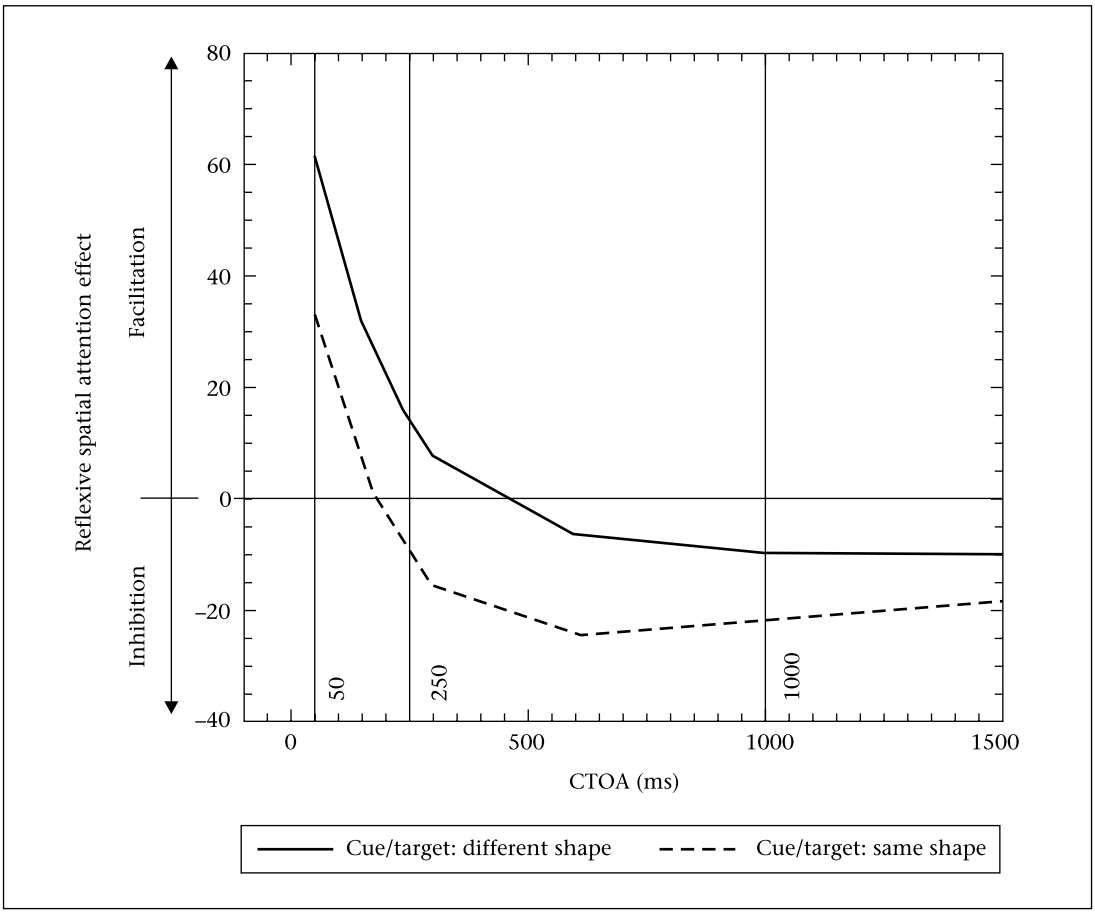
(*Figure 7.13 Continued*)



Note: Panels A and B depict two types of cued conditions (CUED) where the target is presented at the same location as the cue (Location 1 indicated by L1 in the left margin). In Panel A, the target (a circle, activating Neuron 1, light red neuron) has the same shape as the cue, whereas in Panel B the target (a triangle, activating Neuron 2, dark red neuron) has a different shape than the cue. Panel C depicts an uncued condition (UNCUED) where the target is presented at a different location (Location 2 or L2) than the cue (L1). The target in Panel C could be either a circle or triangle, activating either Neuron 3 or 4 (green neurons). For each graph, the activity of each model Neuron is indicated by the broken lines (see figure legend in upper left graph). For simplicity of illustration, activities of only 3 of the neurons are depicted (only Neuron 3 is shown at Location 2). Identical results will be obtained if the target was presented to Neuron 4 instead of Neuron 3 in the uncued condition. The black solid line in each graph indicates the output of the model. The shaded gray region in each graph represents a 50 ms period of time shortly after target presentation, over which the output is integrated for association with the behavioural response to the target (target related output, see Figure 14). A) Simulated output of the model during a cued trial where the target (S2) has the same shape as the cue (S1). Firing traces (relative response magnitude) of model Neurons 1 (light red), 2 (dark red), and 3 (green) in Figure 12 in response to a cue (circle in Location 1, presented at time 0) and target (circle in Location 1) presented at either 50 ms in the first column, 150 ms in the second column, or 1000 ms in the third column. Both cue and target are presented briefly for 30 ms. In panel A, the first peak response of Neuron 1 (light red line), labeled R_0 in the third graph, indicates the magnitude of the normal unadapted response of the neuron to a stimulus, and AR indicates the magnitude of an adapted response of Neuron 1 to the repetition of the same stimulus at three different intervals following the initial stimulus (AR_{50}, AR_{250}, AR_{1000} for CTOAs of 50 ms, 250 ms, and 1000 ms). B) Output of the model during a cued trial where the target (S2) has a different shape than the cue (S1). Firing traces of model Neurons in response to a cue (circle in Location 1) and target (triangle in Location 1). All conventions remain the same as in Panel A. C) Firing traces of model Neurons in response to cue (circle) and target (circle or triangle). Here, the cue is presented at Location 1, whereas the target is presented at Location 2, corresponding to an UNCUED condition.

of the response time). Attentional effects were then computed by comparing the model's output to the target across conditions (uncued mRT minus cued mRT condition) and are illustrated in Figure 7.14 for the two different spatial cueing conditions (same shape of cue and target, dashed line; different shape of cue and target, solid line).

FIGURE 7.14 Simulation of reflexive spatial attention and the influence of shape



Note: To calculate the effect of reflexive attention at a particular CTOA, we compare the target related output (see gray shaded region in the individual graphs of Figure 13) in a cued condition (Figure 13, Panel A: cue and target, same shape, or Panel B: cue and target, different shapes) versus an uncued condition (Panel C). The difference between the target related output in a cued and uncued condition as a function of cue-target onset asynchrony (CTOA) simulates the behavioural effect of reflexive spatial attention. The solid curve shows the simulated reflexive spatial attention effects in a standard attention paradigm in which the cue and target have different shapes (comparing model output in Panels B and C in Figure 13). The dotted curve shows the spatial attention effects when the cue and target have the same shape (comparing model output in Panels A and C in Figure 13). The three black vertical lines denote the three CTOA conditions that are depicted in Figure 13, namely CTOAs of 50, 250, and 1000 ms. Note that behavioural responses are slowed when the shapes of cue and target are the same. As a consequence, at a relatively early CTOA of 250 ms, the standard attentional paradigm (different shape of cue and target, solid curve) results in behavioural facilitation, whereas the same shape attentional condition (same shape of cue and target, dotted curve), results in behavioural inhibition.

We now briefly describe in greater detail the simulation results of the model for a cued trial in which the target has the same shape as the cue (Figure 7.13A). Each of the three graphs in Figure 7.13A illustrates the model's simulation results for 3 different CTOAs (50, 250, and 1000). In each graph, the first peak response of Neuron 1 (light red line; arrow labeled R_0 in the third graph) indicates the magnitude of the normal unadapted response of the neuron to a stimulus cue. For each graph, AR indicates the magnitude of an adapted response (AR) of Neuron 1 to the repetition of the same stimulus (target) at three different cue-target intervals following the initial stimulus (labeled AR_{50}, AR_{250}, AR_{1000} for CTOAs of 50 ms, 250 ms, and 1000 ms). As illustrated in the first graph (CTOA of 50 ms) in Figure 7.13A, the response to the target is the most attenuated, indicated by the relatively small increase in activity associated with presentation of the target (indicated by arrow labeled AR_{50}). In this cued condition, given that the activity of the neuron is high at the time of target presentation, due to temporal proximity of the cue response, even a weak adapted response to the target (second peak of light red line) is greater than the initial cue response (first peak of light red line). More importantly, the output of the model to the target at the shortest CTOA (solid black line during the gray highlighted period in the first graph, Figure 7.13A) is greater than the output to the target on uncued trials (solid black line during the gray highlighted period in the first graph, Figure 7.13C). This period of time corresponds to the period of behavioural facilitation illustrated in Figure 7.14 by the position of the dashed curved line above 0 at a CTOA of 50 ms (indicated by the first vertical line, labeled 50).

At slightly longer CTOAs (second graph of Figure 7.13A), the response to the target begins to recover. The adapted response, indicated by arrow labeled AR_{250}, increases compared to AR_{50}. Nevertheless, in this cued condition, the response to the target (second peak of light red line, second graph, Figure 7.13A) is suppressed and smaller than the neuron's response to the initial cue (first peak of light red line). However, due to a non-adapted response in the uncued location coupled with inhibitory spatial interactions, the neuronal response to a stimulus in an uncued location is actually slightly greater (gray highlighted region of green line, second graph, Figure 7.13C). Together, these effects result in a weaker output of the model in the cued versus uncued condition and, thus, a slower behavioural response to the target in the cued versus uncued condition. This period of time corresponds to the onset of behavioural inhibition or IOR, as illustrated in Figure 7.14 by the position of the dashed curved line below 0 at a CTOA of 250 ms (indicated by the second vertical line, labeled 250).

At even longer CTOAs (third graph of Figure 7.13A), the response of the neuron to the target has largely recovered from adaptation. The adapted response, indicated by arrow labeled AR_{1000}, is now nearly equivalent to the initial response to the cue, arrow labeled R_0. However, in an uncued location (gray highlighted region of green line, third graph, Figure 7.13C), due to persistent adaptation effects and inhibitory spatial interactions, the response of a neuron to a target continues to be greater than the response to a target in

the cued condition (gray highlighted region or second peak of light red line, third graph, Figure 7.13A). Together, these effects result in a weaker output of the model in the cued versus uncued condition and, thus, a slower response to the target. This period of time corresponds to behavioural inhibition or IOR, as illustrated in Figure 7.14 by the position of the dashed curved line below 0 at a CTOA of 1000 ms (indicated by the third vertical line, labeled 1000).

The dynamic properties of these model neurons, including repetition suppression and maintained activity, qualitatively agree with previous reports of neurophysiological recordings in SC, AIT, and LIP. Further, the output of the model to a target presented at a cued location (Figure 7.13A, 13B) compared to an uncued location (Figure 7.13C), at different CTOAs, qualitatively agrees with standard reflexive attentional effects (see curves in Figure 7.14). That is, greater output on cued trials to a repeated stimulus at short intervals results in behavioural facilitation, and reduced output on cued trials to a repeated stimulus at longer intervals results in behavioural inhibition (IOR). Hence, a simple network model composed of shape selective cells with an adaptive mechanism appears to be sufficient to explain reflexive spatial attentional cueing effects.

Prediction of the Model: Effect of Shape on Reflexive Spatial Attention

Although repetition suppression effects appear to be sufficient to explain reflexive spatial attentional cueing effects, cortical brain regions are sensitive to and selective for different properties and previous studies have demonstrated that repetition suppression effects are specific and dependent on the stimulus properties represented, such as shape (Lehky and Sereno, 2007). If such suppression effects in these cortical areas result in reflexive attentional effects, then some form of reflexive spatial attention should be sensitive to the shape of the cue and target. To model the effects of the cue and target shape on reflexive attention, we compared the output of the model when the target had the same shape as the cue (Figure 7.13A) versus when it had a different shape (Figure 7.13B). As illustrated in Figure 7.14, the solid curve shows behavioural results of the model for a standard reflexive attention task, where cue and target shape differ. Output from the model produces facilitation at short CTOAs and inhibition at longer CTOAs. However, when the cue and target have the same shape, early spatial facilitation is reduced, resulting in an earlier onset of IOR (Figure 7.14, dashed curve). The model thus predicts that some spatial attention effects may depend on the visual similarity of the cue and target.

Spatial Attention is Influenced by the Shape Similarity of the Cue and Target

Some previous reports have suggested that stimulus attributes of the cue and target, such as colour, orientation, and shape may affect spatial attentional effects. Kwak and Egeth

(1992) showed that response times for CTOAs ranging from 300 to 900 ms were faster when the orientation of cue and target were the same. On the other hand, Riggio, Patteri, and Umilta (2004) showed that response times at 250 and 500 ms were slowed when the shape of cue and target were the same. Studies examining letter (Corballis and Armstrong, 2007) and word (Kanwisher, 1987) repetitions have similarly demonstrated a substantial inhibitory effect on recognition performance for repetition intervals between 100 and 700 ms. In a recent series of experiments, we also showed that the shapes of cue and target influence reflexive spatial selective attention. At some CTOAs, the same shape of cue and target reduces or even eliminates the early facilitation and agrees qualitatively with the predictions of the model as illustrated in Figure 7.14 (Patel et al., 2007).

IMPLICATIONS OF WIDESPREAD REPETITION SUPPRESSION EFFECTS

A Simple Adaptive Mechanism as the Basis of Reflexive Spatial Attention

We hypothesize that reflexive spatial attentional effects, including effects of both a cue's location and its shape on the behavioural response to a following target, can be explained by repetition suppression. We created a model consisting of neurons whose dynamic properties were similar to those of neurons in area AIT, LIP, and SC, and found that the model's simulations qualitatively agree with psychophysical data (Patel et al., 2007), suggesting that these properties are sufficient to explain spatial attentional cueing effects.

Repetition Suppression as a Ubiquitous and Distributed Property in the Brain

As reviewed above, repetition suppression effects have been shown repeatedly in several areas in the ventral stream. Such effects for 2D shapes are also present in LIP, a high-level dorsal stream area (Lehky and Sereno, 2007). Repetition suppression appears to be a ubiquitous and distributed reflexive response property occurring in many areas of the brain.

Many Forms of Reflexive Spatial Attention and IOR

Given that different brain regions are sensitive and selective for different stimulus attributes, we suggest that suppression effects may be specific and dependent on the stimulus properties represented in each area. If repetition suppression is related to the manifestation of reflexive spatial attention as it is in the SC, then there may be many forms of IOR. Attentional effects, then, may depend on the stimulus properties and organization of stimulus properties represented in different brain areas. In support of this contention, in a recent series of experiments, we show that the shape of cue and target can influence reflexive spatial selective attention (Patel et al., 2007).

LIP as the Upstream Source of IOR in SC

As reviewed above, Dorris et al. (2002) suggested that the attenuated activity in the SC to a repeated stimulus reflects a signal reduction that has taken place upstream of the SC, perhaps in posterior parietal cortex. We have demonstrated that neurons in LIP, an area in posterior parietal cortex with heavy projections to the SC, show reduced responses to a repeated stimulus. Accordingly, LIP could be the upstream source of the attenuated signals in SC. Alternatively, as we demonstrate with our model using a simple adaptive mechanism, the neurons need not incur any additional suppressed signals to exhibit a suppressed or adapted response. Hence, both areas may create unique and independent neural correlates of reflexive attention. Indeed, we have recently demonstrated that cells in LIP represent reflexive attentional and mnemonic properties more robustly than voluntary ones (Sereno and Amador, 2006).

Facilitation versus Inhibition

Because the neural mechanisms underlying reflexive attentional cueing effects were not well understood, some previous investigators suggested that facilitation and IOR effects due to reflexive spatial attention may be independent effects that occur simultaneously, but whose magnitudes follow different time courses (Klein, 2000; Ro and Rafal, 1999; Tipper et al., 1997). We demonstrate that, with our model composed of neurons with a simple adaptive mechanism, we can elicit either increased responses to the target (behavioural facilitation) or suppressed responses to the target (behavioural inhibition). We also show that, by manipulating the shapes of the cue and target, we can induce an additional inhibitory cueing effect. Thus, while not ruling out the possibility of independent facilitatory and inhibitory mechanisms, our model results, showing facilitation, inhibition, and even modulations that appear specific to either facilitation or inhibition, do not necessitate independent mechanisms.

Comparison to Previous Computational Models of Visual Attention

Several elaborate computational models of visual attention attempt to account for many aspects of attention including both reflexive and voluntary processes (for review, Itti and Koch, 2002). Our model differs in several respects. First, the model is focused and restricted. We attempt to explain only reflexive spatial attentional effects. Second, most previous computational models of attention propose a unique "saliency" or "master" map (for example, Koch and Ullman, 1985) that is used to control and maintain a single attentional focus. Although many models are based on a saliency map, Desimone and Duncan (1995) have argued that saliency is not explicitly represented by neurons in a specific saliency map, but instead is implicitly encoded in a distributed modulatory manner

across various feature maps. We propose here a mechanism for reflexive spatial attention that is widespread in the brain and does not require implementation in a unique master saliency map. Additionally, in order to allow a model to rapidly shift attentional focus without being bound to attend only to the location of maximal saliency at any given time, various computational models have implemented IOR as a trigger of transient inhibitory conductances in the saliency map at the currently attended location (Itti and Koch, 2002). We propose here a mechanism, widespread in the brain, and argue that reflexive spatial attentional effects are specific and local to the areas that are responding.

CONCLUSIONS

In sum, the first neurophysiological evidence recorded from neurons in the SC suggests that the second presentation of a stimulus results in a reduced neuronal response. The magnitude of the reduced response is correlated with behavioural response and IOR. We suggest here that this reduced response of neurons in SC is similar to repetition suppression effects previously reported in ventral stream areas. We also show that repetition suppression effects are present and of equal magnitude in a dorsal stream area, LIP, that is involved in eye movements and attention and also has dense projections to the SC. Such effects may be a pervasive feature of many brain regions. Further, given that multiple brain regions represent different aspects of visual stimuli, repetition suppression effects are likely specific to particular features that each area represents. For this reason, they have become a powerful tool in fMRI research to explore stimulus-specific neuronal representations. We have developed a simple neural model showing that repetition suppression effects can account for spatial and shape dependent reflexive spatial attentional cueing effects, providing a plausible neurophysiological mechanism for reflexive spatial attention that accounts for the time course and valence (facilitation and inhibition) of both spatial and shape effects.

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Figure 1

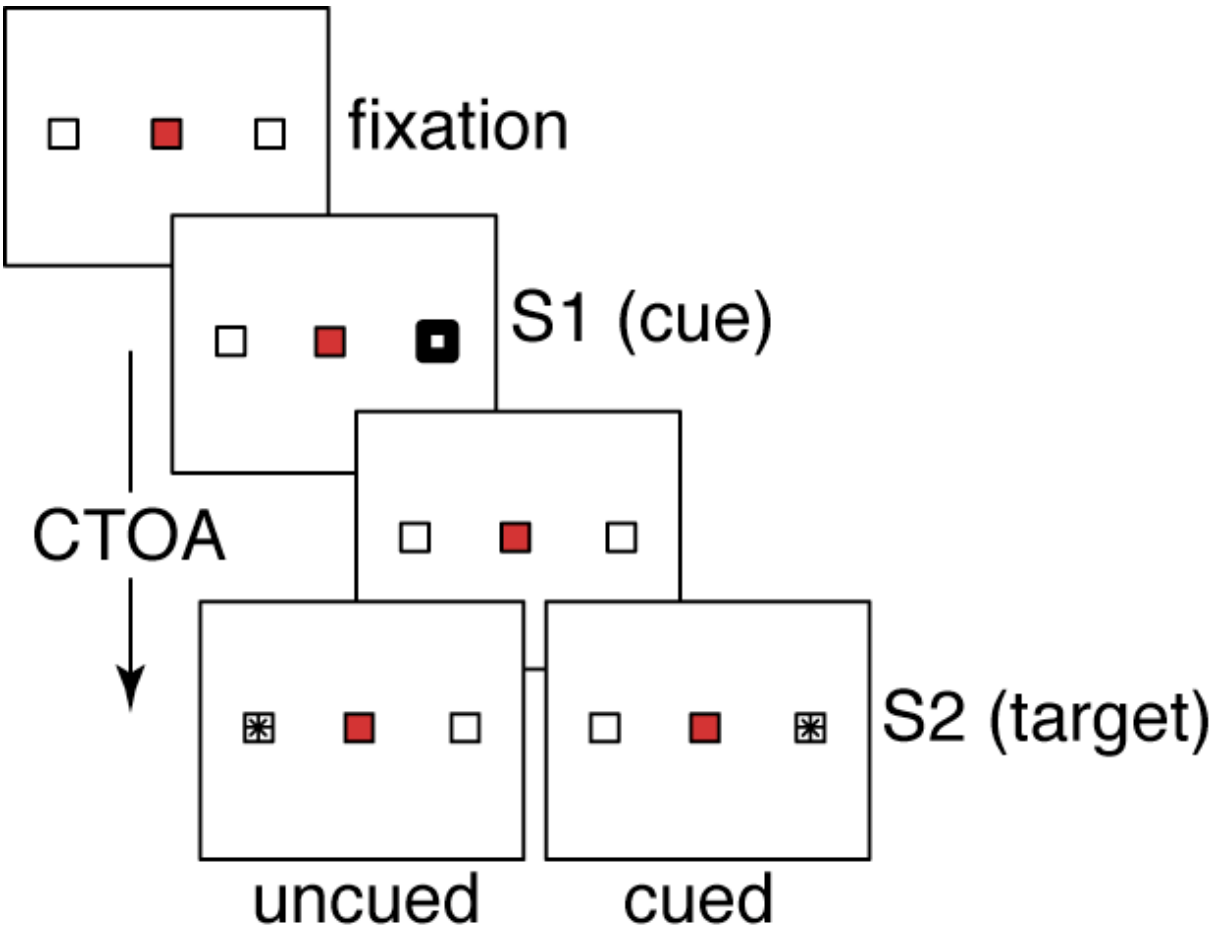


Figure 2

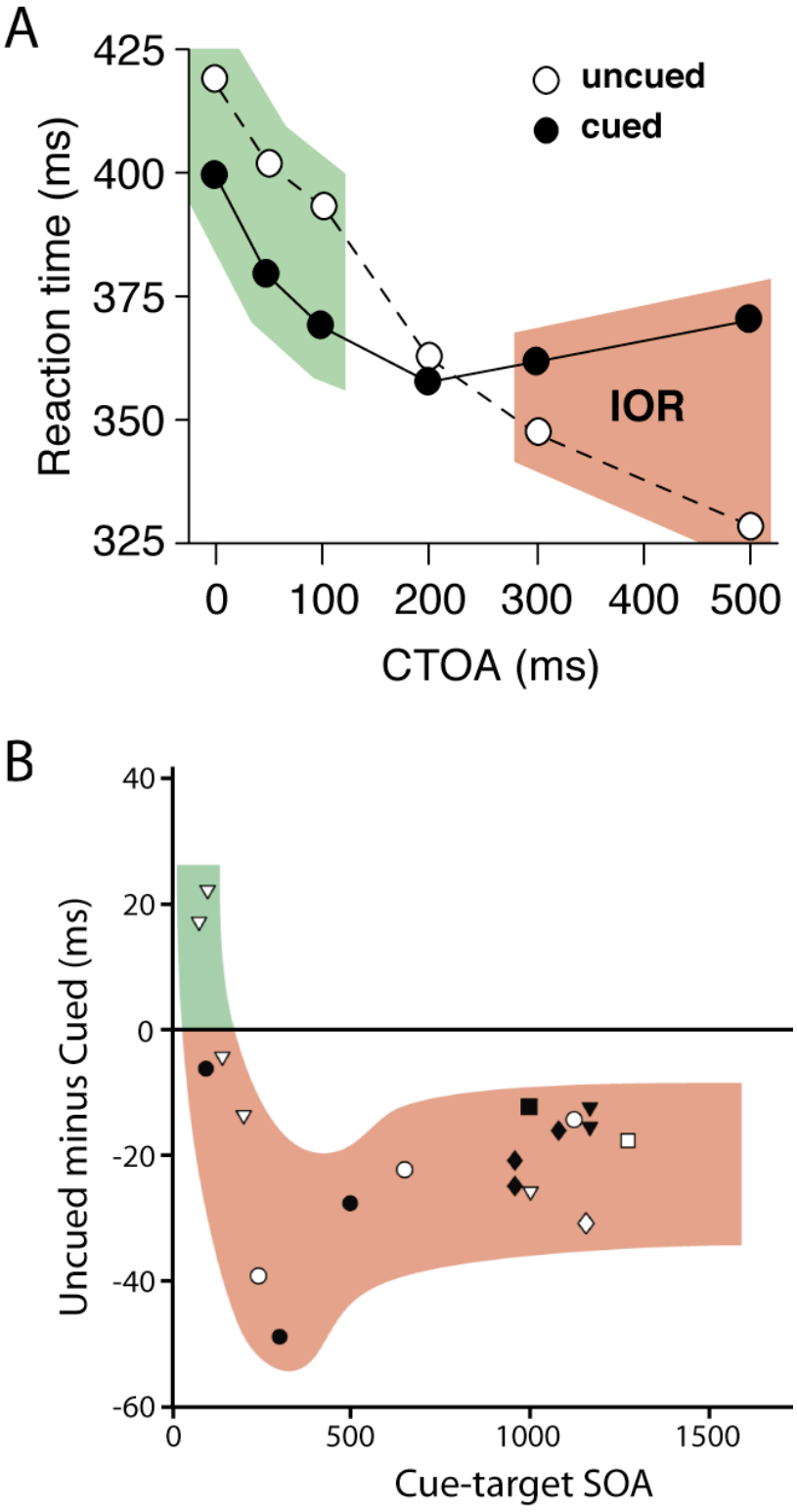
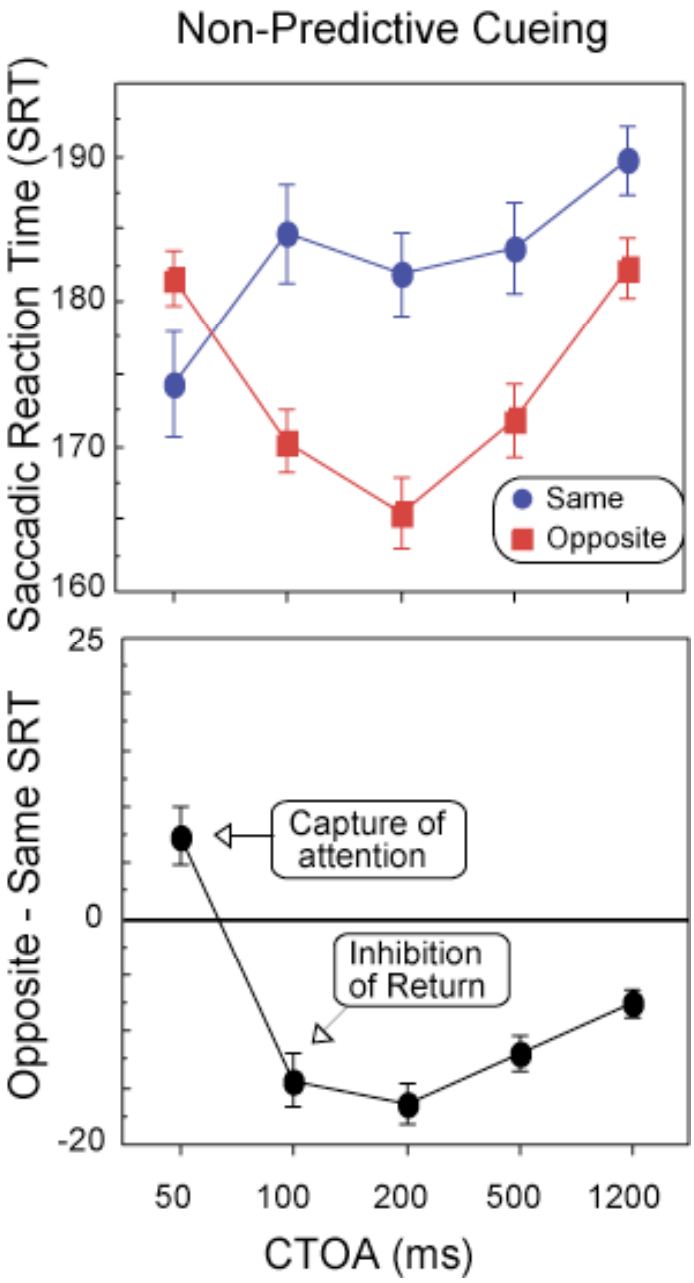

A
425
400
375
350
325
Reaction time (ms)
uncued
cued
IOR
0
100
200
300
400
500
CTOA (ms)
B
40
20
0
-20
-40
-60
Uncued minus Cued (ms)
0
500
1000
1500
Cue-target SOA

Figure 3


Non-Predictive Cueing
Saccadic Reaction Time (SRT)
190
180
170
160
Same
Opposite
Opposite - Same SRT
25
0
-20
Capture of attention
Inhibition of Return
50
100
200
500
1200
CTOA (ms)

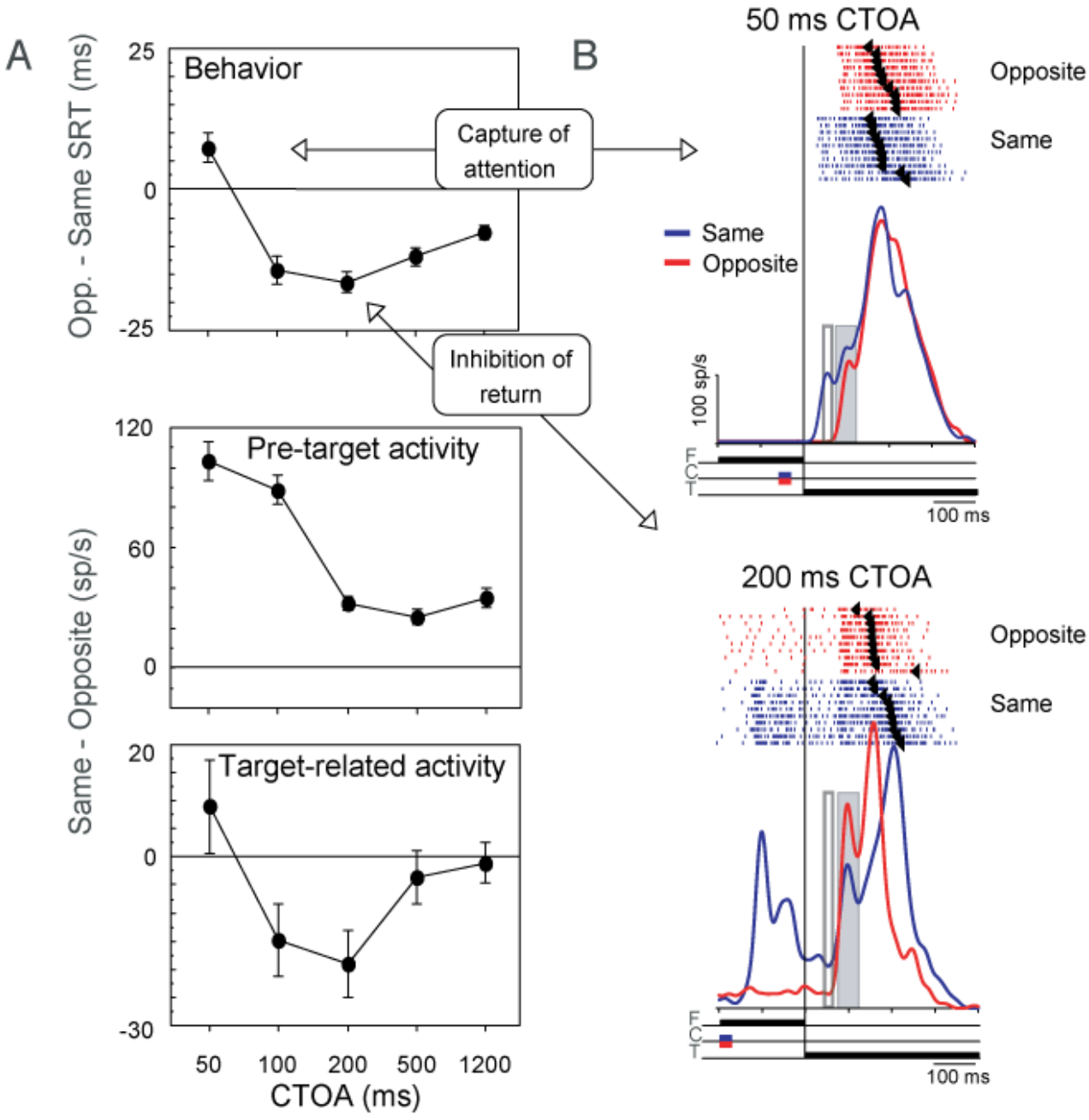

A
B
Behavior
Opp. - Same SRT (ms)
25
0
-25
Capture of attention
Inhibition of return
Pre-target activity
Same - Opposite (sp/s)
120
60
0
Target-related activity
20
0
-30
50
100
200
500
1200
CTOA (ms)
50 ms CTOA
Opposite
Same
Same
Opposite
100 sp/s
100 ms
200 ms CTOA
Opposite
Same
100 ms

Figure 5

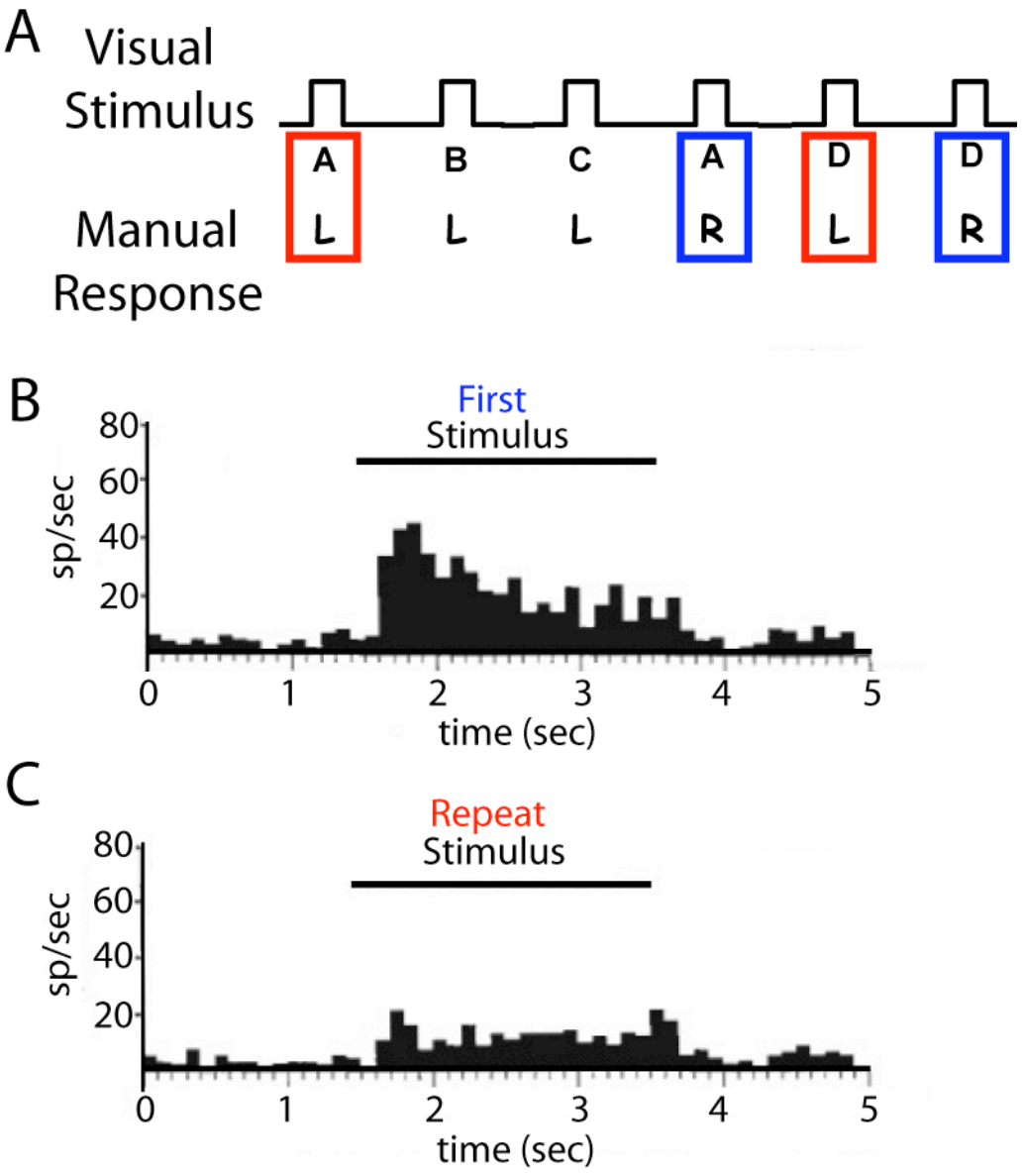

A
Visual Stimulus
A B C A D D
Manual Response
L L L R L R
B
First Stimulus
sp/sec
80
60
40
20
0 1 2 3 4 5
time (sec)
C
Repeat Stimulus
sp/sec
80
60
40
20
0 1 2 3 4 5
time (sec)

Figure 6

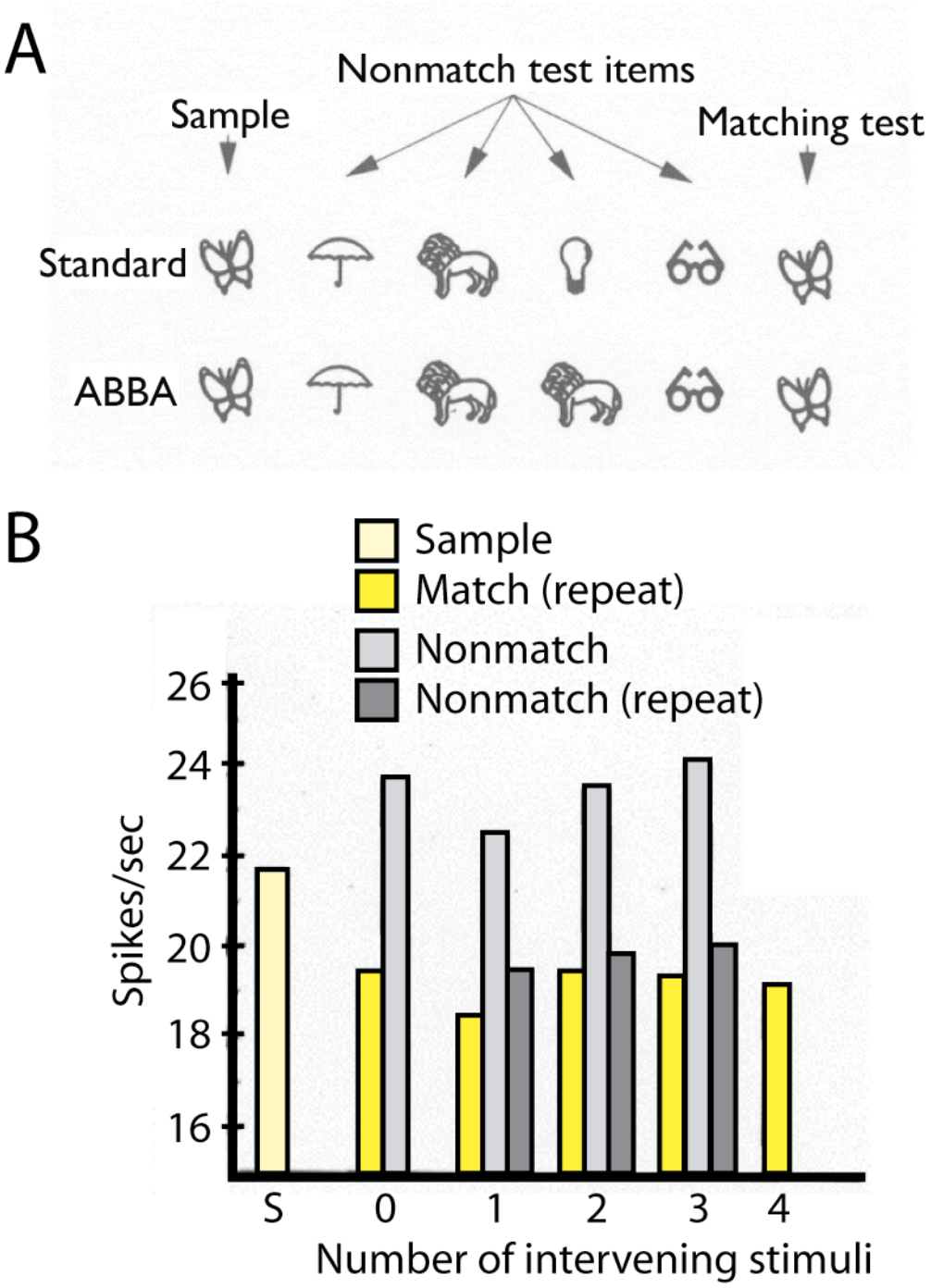

A
Nonmatch test items
Sample
Matching test
Standard
ABBA
B
Sample
Match (repeat)
Nonmatch
Nonmatch (repeat)
Spikes/sec
26
24
22
20
18
16
S
0
1
2
3
4
Number of intervening stimuli

Figure 7

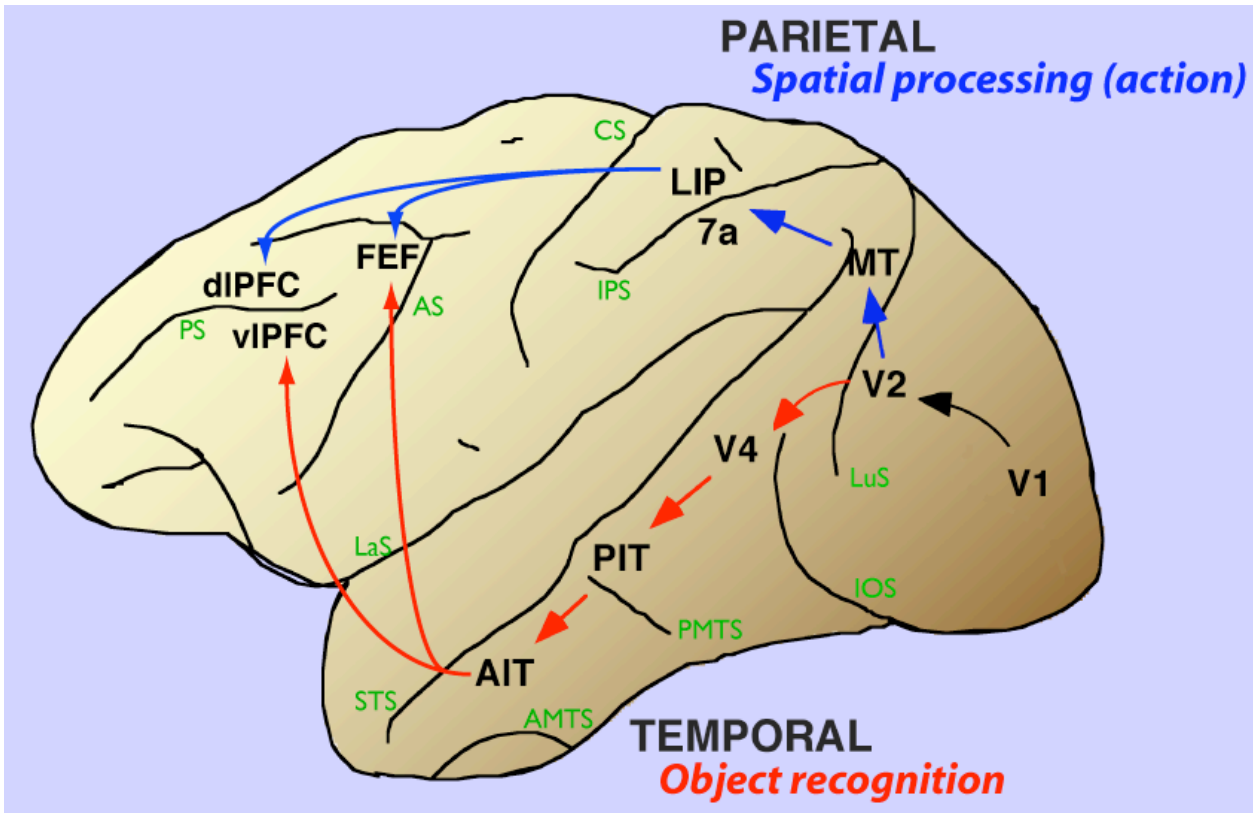

PARIETAL
Spatial processing (action)
CS
LIP
7a
MT
FEF
dlPFC
PS
vlPFC
AS
IPS
V2
V4
LuS
V1
LaS
PIT
IOS
PMTS
AIT
STS
AMTS
TEMPORAL
Object recognition

Figure 8

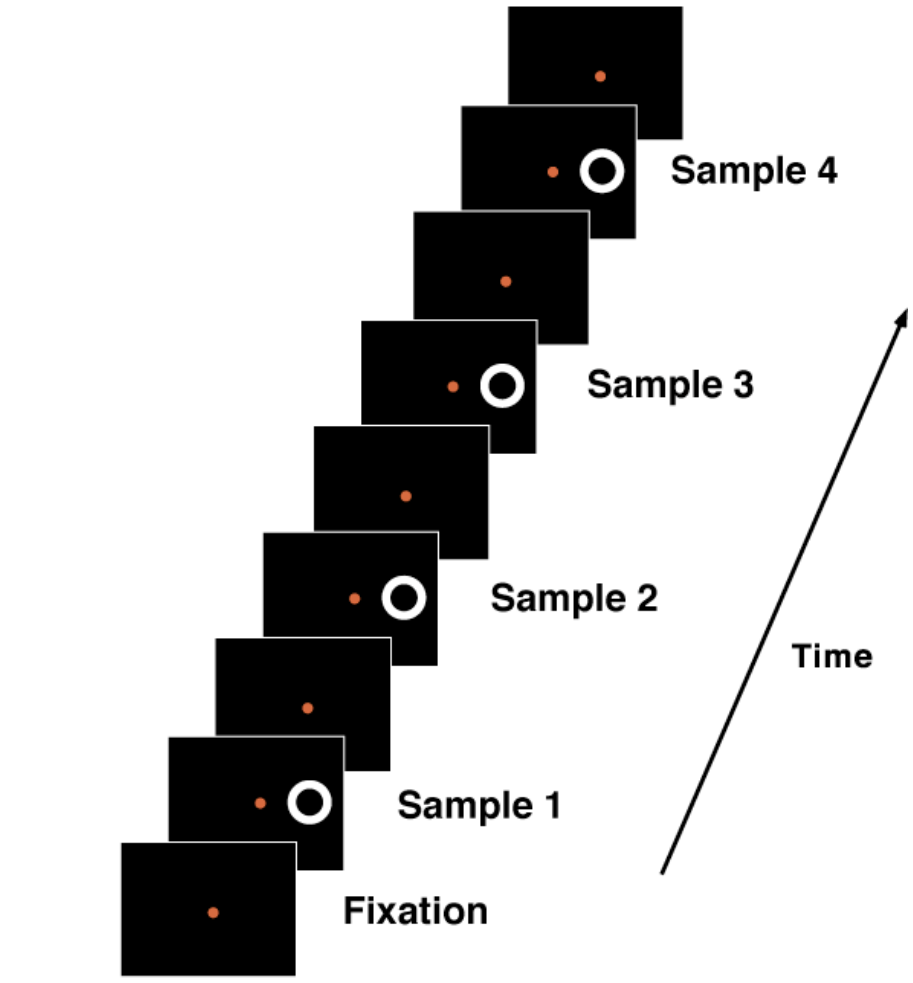

Sample 4
Sample 3
Sample 2
Sample 1
Fixation
Time
Fixation Task

Figure 9

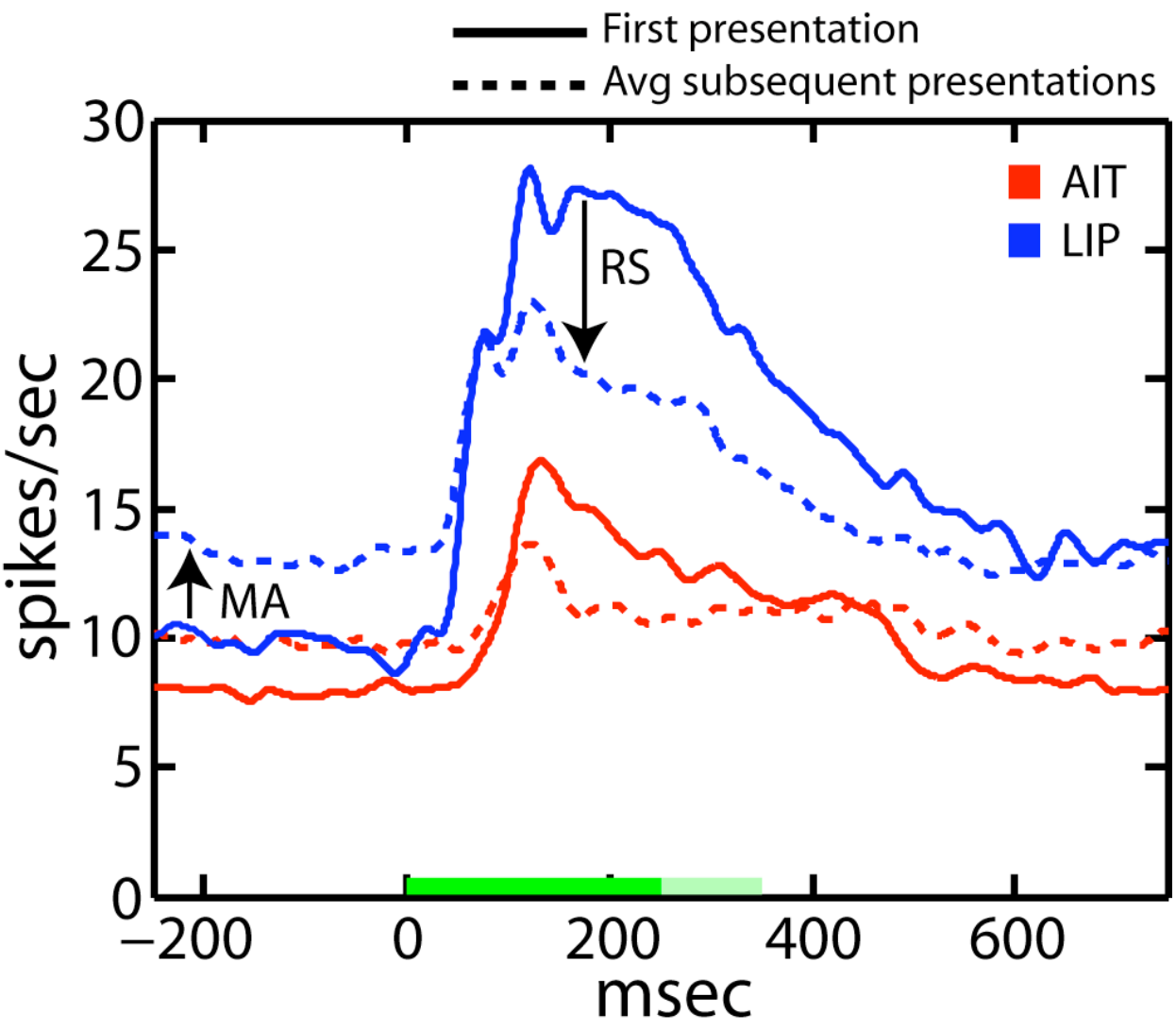

First presentation
Avg subsequent presentations
AIT
LIP
RS
MA
spikes/sec
30
25
20
15
10
5
0
−200
0
200
400
600
msec

Figure 10

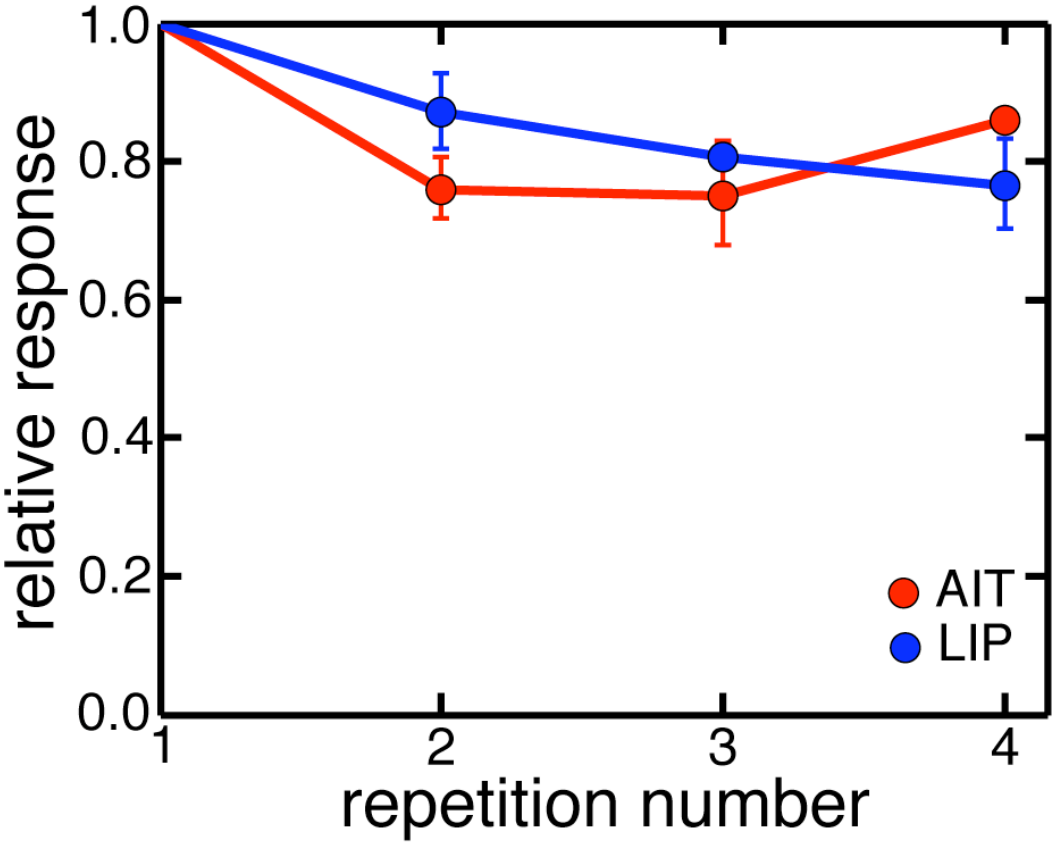

1.0
0.8
0.6
0.4
0.2
0.0
relative response
1
2
3
4
repetition number
AIT
LIP

Figure 11

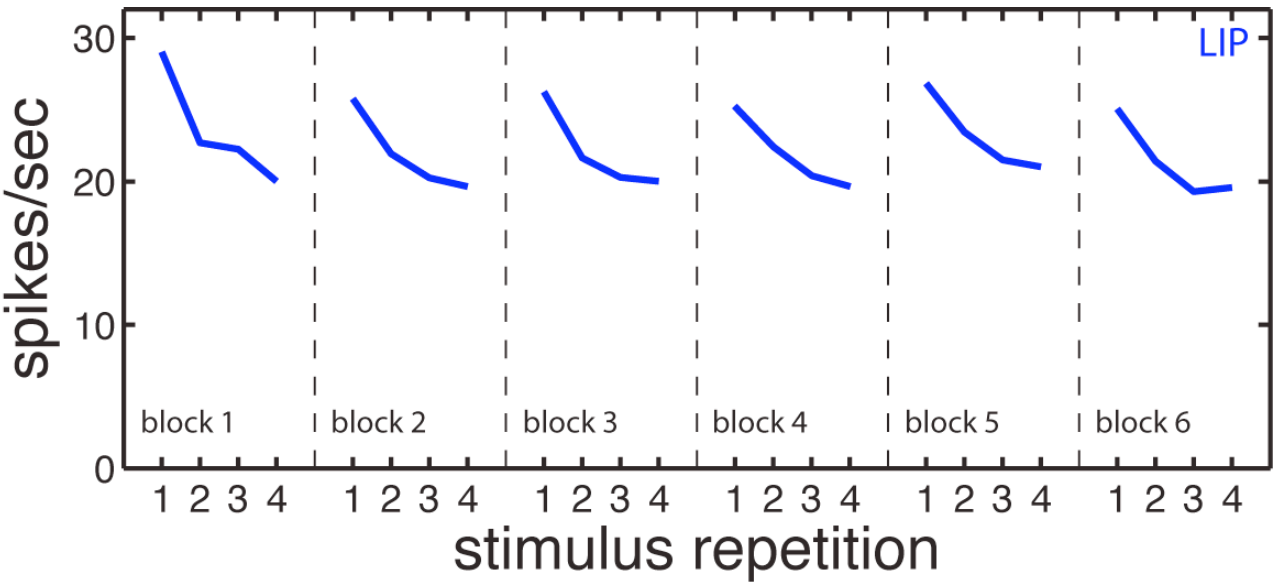

LIP
spikes/sec
30
20
10
0
block 1
block 2
block 3
block 4
block 5
block 6
1 2 3 4
1 2 3 4
1 2 3 4
1 2 3 4
1 2 3 4
1 2 3 4
stimulus repetition

Figure 12

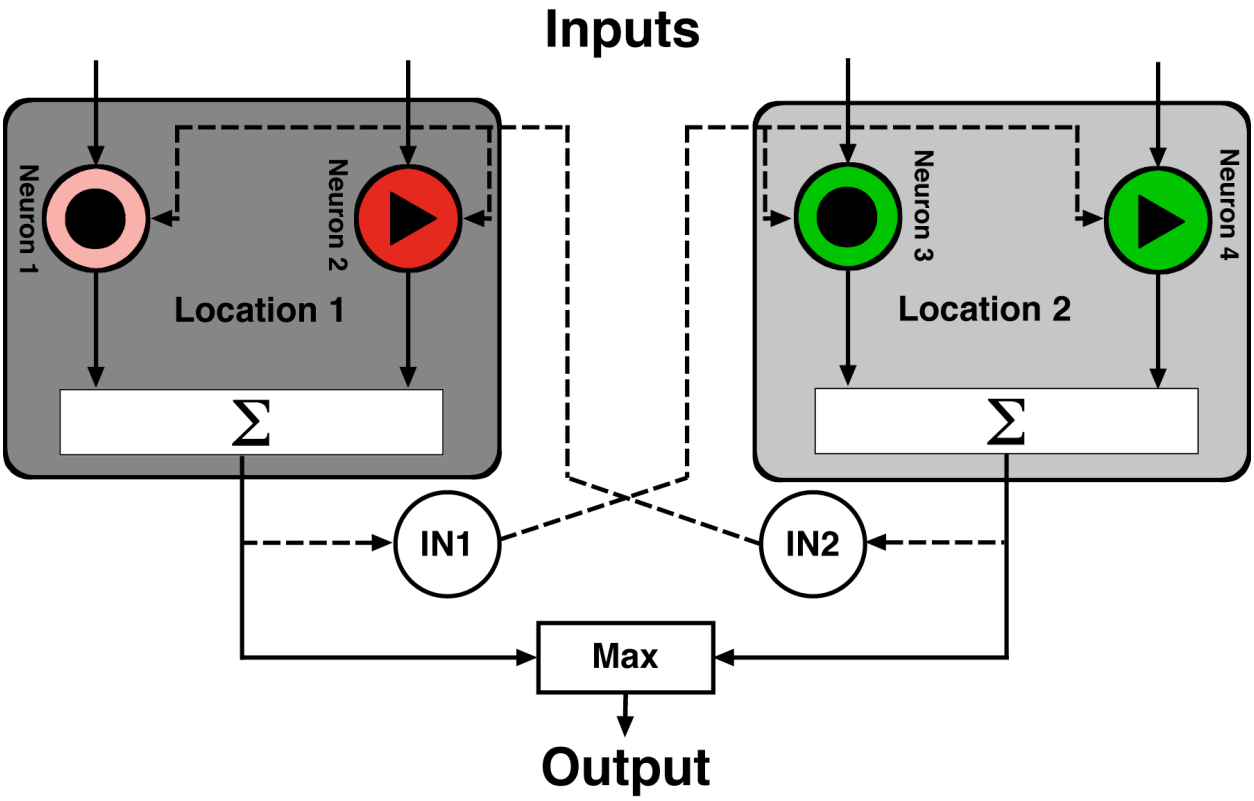

Inputs
Neuron 1
Neuron 2
Location 1
Σ
Neuron 3
Neuron 4
Location 2
Σ
IN1
IN2
Max
Output

Figure 13

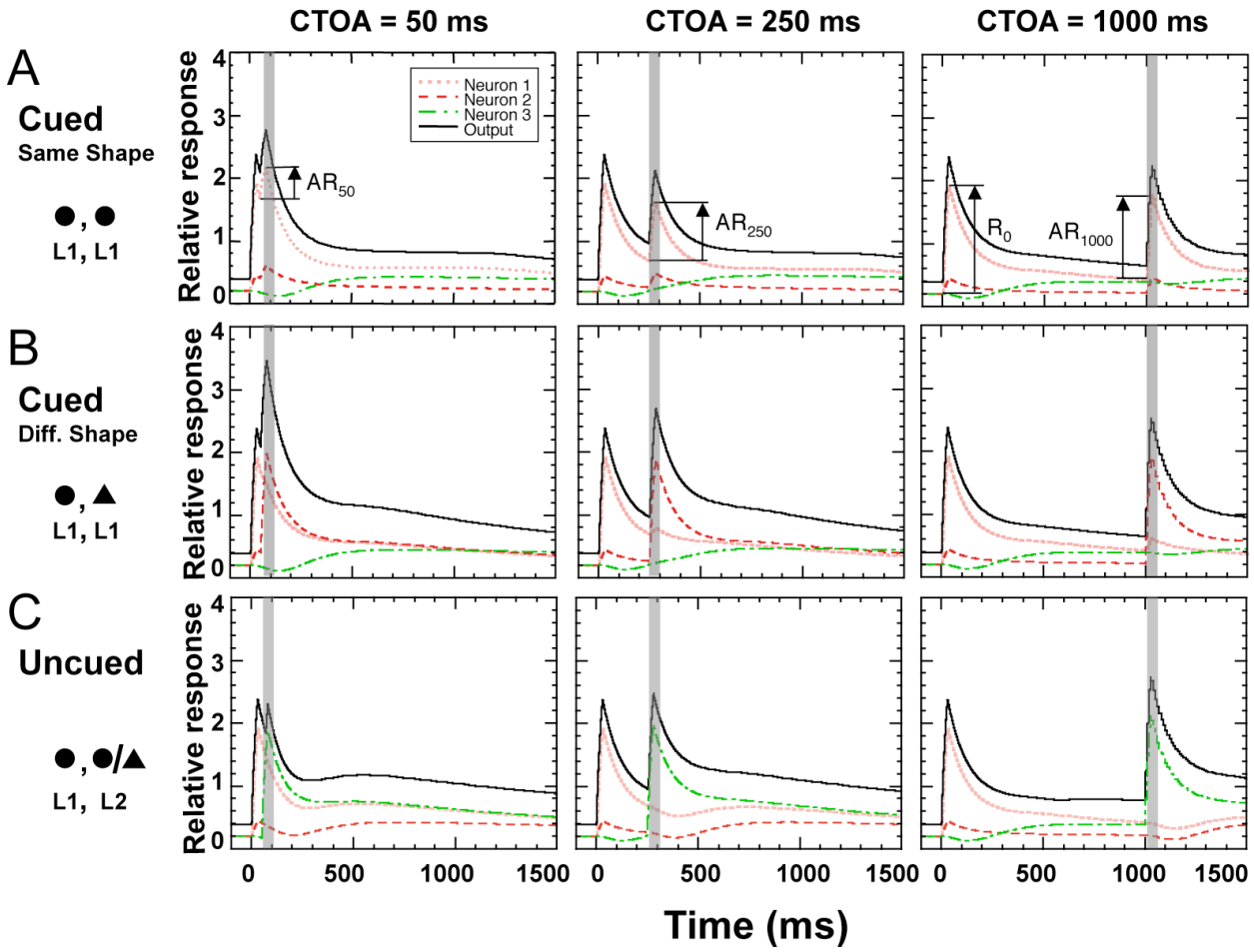
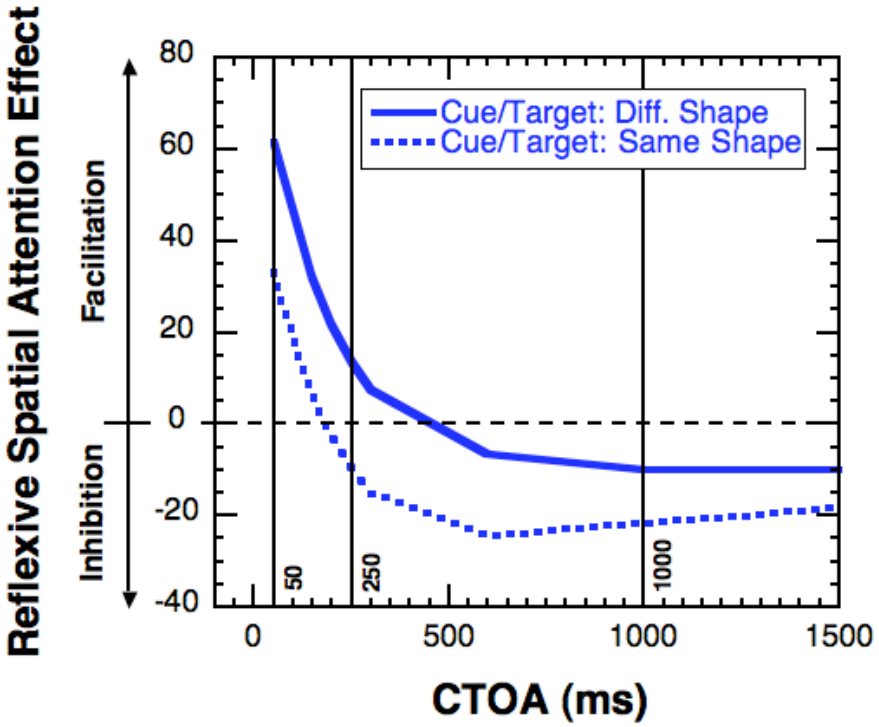

CTOA = 50 ms
CTOA = 250 ms
CTOA = 1000 ms
A
Cued
Same Shape
●, ●
L1, L1
B
Cued
Diff. Shape
●, ▲
L1, L1
C
Uncued
●, ●/▲
L1, L2
Neuron 1
Neuron 2
Neuron 3
Output
AR50
AR250
R0
AR1000
Relative response
0
1
2
3
4
0
500
1000
1500
Time (ms)

Figure 14


Reflexive Spatial Attention Effect
Facilitation
Inhibition
80
60
40
20
0
-20
-40
0
500
1000
1500
CTOA (ms)
50
250
1000
Cue/Target: Diff. Shape
Cue/Target: Same Shape