

Neurophysiological Correlates of the Reflexive Orienting of Spatial Attention

Jillian H. Fecteau, Andrew H. Bell, Michael C. Dorris, and Douglas P. Munoz

ABSTRACT

There are two reflexive biases in orienting attention that assist in the exploration of the visual scene. A distinct object will draw, or *capture*, spatial attention to its locus. After this object has been inspected (and deemed irrelevant), *inhibition of return* prevents its repeated inspection. Here, we describe the neurophysiological correlates of these biases in orienting attention. In the superior colliculus, both originate from changes in sensory processing—the capture of attention is linked to a strong neural representation of a visual target, whereas inhibition of return is associated with a weak representation of this target. We describe how changes in this sensory signal may produce changes in behavior and can explain the typical and anomalous findings associated with these biases in reflexively orienting attention.

Figure 64.1a illustrates the cue-target task that elicits both the capture of attention and inhibition of return (Posner and Cohen, 1984). In this task, a flash of light in peripheral visual field (the cue) is followed by a second visual stimulus (the target) that appears at the same or opposite location as the cue. The cue serves as the distinct, or salient, object. Responding to the target probes the consequences of the cue on orienting attention toward a new object (i.e., the target).

Manipulating the time between the onset of the cue and target (cue-target onset asynchrony, CTOA) produces a cross-over interaction, as shown in the mean correct saccadic reaction time of 16 human (see Fig. 64.1b, left) and 2 monkey (right) observers. This may be seen more clearly in the subtraction plot illustrated in Fig. 64.1c (positive values signify the advantage in

saccadic reaction time when the cue and target appear at the same location, whereas negative values signify the advantage in saccadic reaction time when the cue and target appear at opposite locations). At the short CTOAs, the participants responded faster when the cue and target appeared at the same location. This represents the capture of attention—the compulsion that observers have to inspect abrupt changes in the visual scene (Jonides, 1981; see Chapter 69). At longer CTOAs, the participants responded more slowly when the cue and target appeared at the same location. This represents inhibition of return (see Chapter 16), the tendency of observers to favor new locations in the visual scene, as opposed to previously inspected locations (see also Posner and Cohen, 1984; Posner et al., 1985). Although both humans and monkeys produced similar patterns of behavior, the timing of the cross-over was shifted forward for monkeys; this originates from the repeated testing of monkeys on this task (Dorris et al., 2002).

As the monkeys performed this task, we monitored the activity of visuomotor neurons in the intermediate layers of the superior colliculus (SC). The SC is of particular interest when exploring the neurophysiological basis of reflexive orienting because it may produce inhibition of return (Posner et al., 1985; Sapir et al., 1999). In addition, its visuomotor neurons produce three distinct neural signals that could carry these biases in orienting attention. Each neuron discharges in response to the appearance of a visual stimulus in and the initiation of a saccade generated to its response field (see Munoz et al., 2000; Munoz and Fecteau, 2002 for reviews). Moreover, visuomotor neurons can have low-frequency activity that is modulated by attention, motor preparation, and target selection (e.g., Glimcher

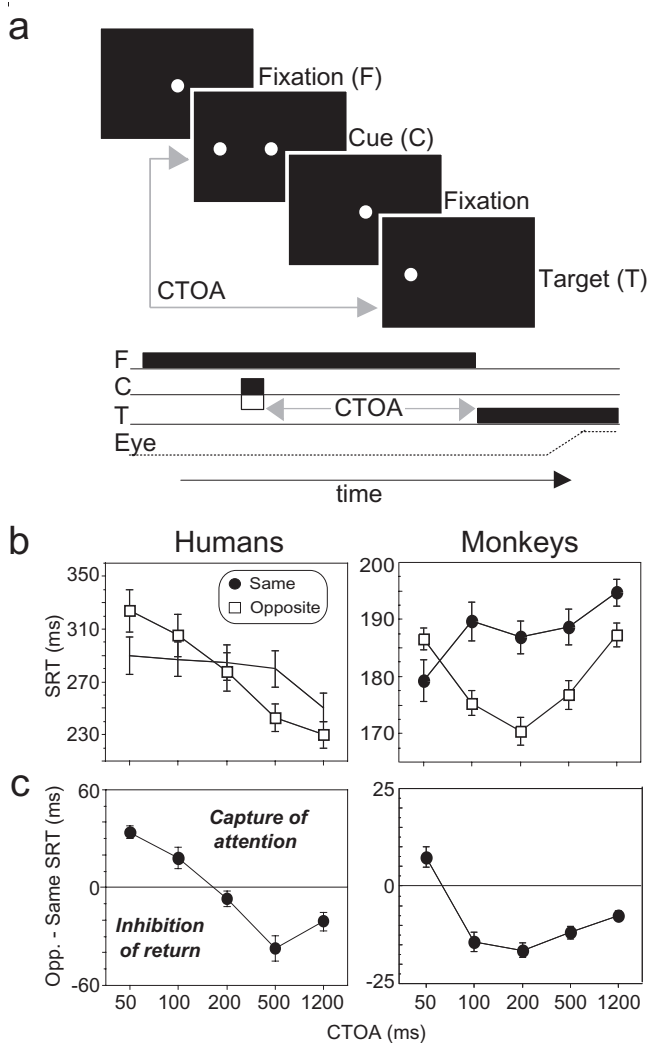


FIGURE 64.1 a. An illustration of the cue-target paradigm used in these studies. Observers fixated a central fixation marker during the presentation of a peripheral cue. A target (T) appeared (fixation marker disappeared simultaneously) and the monkey generated an eye movement to the target's location. The cue and target could appear at the same or opposite locations. The time between cue and target onset (cue-target onset asynchrony: CTOA) was manipulated. **b.** Mean correct saccadic reaction times for human (left) and monkey (right) observers when the target appeared at the *same* (filled circle) and *opposite* (squared) locations as the cue across the CTOAs tested (adapted from Fecteau et al., in submission). **c.** Subtraction plot showing the differences between same and opposite cueing conditions for both groups of participants.

and Sparks, 1992; Basso and Wurtz, 1997; Dorris and Munoz, 1998).

Of these three candidates, only the sensory response to the target (peak target-related activity; see Fig. 64.2a, right) mimicked the changes observed in orienting behavior (left). Stronger target-related activity was obtained at the 50ms CTOA, whereas weaker target-

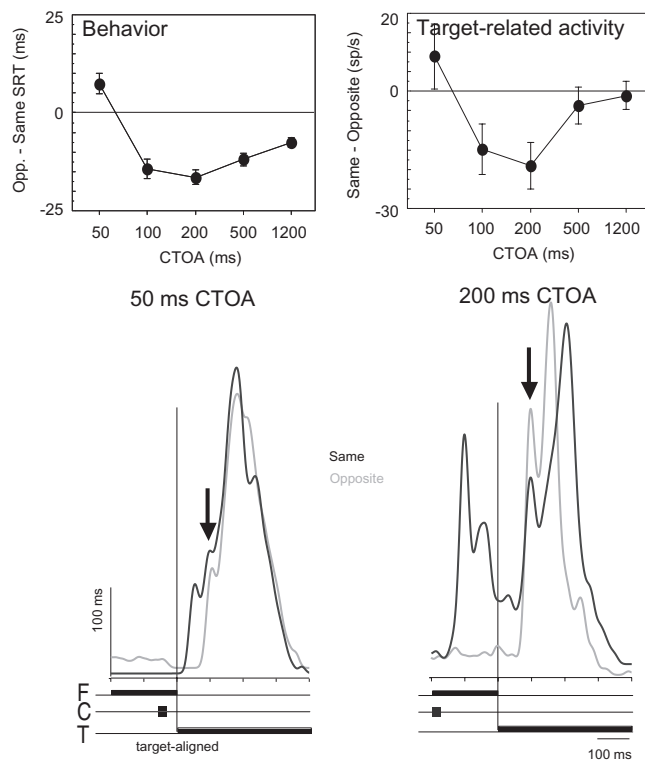


FIGURE 64.2 a. Differences in saccadic reaction time (left) and the corresponding changes in the target-related response (right). **b.** Representative example of the activity of a single neuron at the 50 ms CTOA when the capture of attention was obtained in behavior. **c.** Representative example of the activity of a single neuron at the 200 ms CTOA when inhibition of return was obtained in behavior (adapted from Fecteau et al., 2003).

related activity was obtained at longer CTOAs (≥ 100 ms) when the cue and target appeared at the same location.

In addition, a strong correlation was obtained between target-related activity and saccadic reaction time on a trial-by-trial basis for each neuron, with stronger target-related activity associated with shorter reaction times and weaker target-related activity linked to longer reaction times (Bell et al., 2004; Dorris et al. 2002; Fecteau et al., 2004). A similar relationship was not observed for other neurophysiological signals (pretarget activity or for saccade-related activity) and behavior (Fecteau et al., 2004).

Demonstrating that changes in target-related activity link to the capture of attention and inhibition of return does not reveal what is responsible for these changes. To provide some insight into this issue, we show the activity of two representative neurons. At the 50 ms CTOA (see Fig. 64.2b), target-related activity was stronger because the appearance of the cue was still eliciting a response in the neuron (black trace). So, when the target-related signal entered (see Fig. 64.2b,

black arrow), it summed with the residual activity from the cue, enhancing its peak compared to when the cue appeared at the opposite location (gray trace, Bell et al., 2002; Fecteau et al., 2004). By contrast, at the 200ms CTOA (see Fig. 64.2c), target-related activity was attenuated when the cue appeared at the same location as the target (black trace) than when it appeared at the opposite location (gray trace; Dorris et al. 2002; Bell et al., 2004; Fecteau et al., 2004).

One intriguing feature of the pattern of neural activity obtained at the 200ms CTOA was that the neuron was more excitable after the appearance of the cue (neural activity was elevated before the visual target was registered by the neuron; black trace above gray trace). This effect, observable in most visuomotor neurons in our sample, is somewhat counterintuitive because elevated pretarget activity is associated with faster, not slower, reaction times (Dorris and Munoz, 1998).

This observation forces us to reevaluate the role of the SC in the active generation of inhibition of return. Previously, it was hypothesized that the SC produces inhibition of return because it is eliminated after the SC is lesioned (Posner et al., 1985; Sapir et al., 1999). However, our neurophysiological data indicate that the SC is facilitated after the appearance of the cue (evidenced through elevated pretarget activity) and that the *incoming* target-related response is weakened. If this interpretation is accurate, then saccades initiated through other means should be facilitated when generated to the same location as the cue.

To test this hypothesis, we compared saccadic reaction times in two conditions: when monkeys initiated a saccade to the visual target (75% of the trials; Fig. 64.3a) and when weak electrical stimulation drove a saccade to the same location (25% of the trials; Fig. 64.3b). When using electrical stimulation, the time required to evoke the saccade depends on the level of neural excitability at the time of stimulation (Munoz et al., 2000). In line with our expectations, electrical stimulation produced the opposite pattern of saccadic reaction times (see Fig. 64.3b), than did visual targets (see Fig. 64.3a). This indicates that the incoming target-related signal, as opposed to active inhibition within the SC, is responsible for inhibition of return (Dorris et al., 2002).

At what point along the sensory-to-motor axis does the weakening of the target-related response occur? Although we cannot answer this directly, we have obtained evidence indicating that it originates early on when using this cue-target task. The SC consists of two functionally distinct subregions—the superficial and the intermediate layers. Up to now, we have described changes in neural activity in the intermediate layers,

which receives its inputs from widespread cortical areas, including the frontal eye fields and the lateral intraparietal area, and subcortical areas, including regions of the basal ganglia and thalamus (reviewed in Munoz and Fecteau, 2002). By contrast, the superficial layers receive input from visual areas early in sensory processing, such as V1 and the retina (e.g., Lui et al., 1995; Pollack and Hickey, 1979).

Comparing these functional layers revealed that weaker target-related activity was observed in both (Dorris et al., 2002; Fecteau and Munoz, in submission). This indicates that the attenuation of this target-related signal occurs early (i.e., as early in processing as V1) and is propagated throughout the entire oculomotor network and, perhaps, the entire dorsal visual stream (Fecteau et al., 2004; Robinson et al., 1995). Indeed, weak target-related activity has been observed during similar tasks in the lateral intraparietal area (Robinson et al., 1995) and area 7a, as well (Constantinidis and Steinmetz, 2001; Steinmetz et al., 1994). Area 7a is not strictly a member of the oculomotor network (Andersen et al., 1990).

Taken together then, the changes in reaction times associated with the capture of attention and inhibition of return correlate with changes in the neural salience of the visual target. Both may be viewed as the interactions of sensory stimuli in the cue-target task. Strong target-related activity, linked to the capture of attention, originates from the summation of cue- and target-related activities. Weak target-related activity, linked to inhibition of return, originates at an early stage in sensory processing. Similar findings have been demonstrated in human electrophysiology studies (see Chapter 36). This raises an interesting question—what happens when the sensory signals linked to the cue and target do *not* interact?

In the intermediate and deep layers of the superior colliculus, sensory input from several modalities impinges upon its neurons, including audition (Wallace et al., 1996; Bell et al., 2001). However, unlike the robust activity elicited by visual stimuli, auditory stimuli elicit weaker responses that are registered much sooner after the presentation of the auditory stimulus (Wallace et al., 1996; Bell et al., 2001). These features have important consequences with regard to the capture of attention. Because the neural activity linked to the auditory stimulus will have passed before the neural activity linked to the visual target enters, there is little opportunity for these signals to sum and produce the capture of attention. Regarding the mechanisms responsible for inhibition of return, cross-modal interactions between auditory and visual stimuli occur at a later stage along this sensory-to-motor axis compared to the superficial layers of the

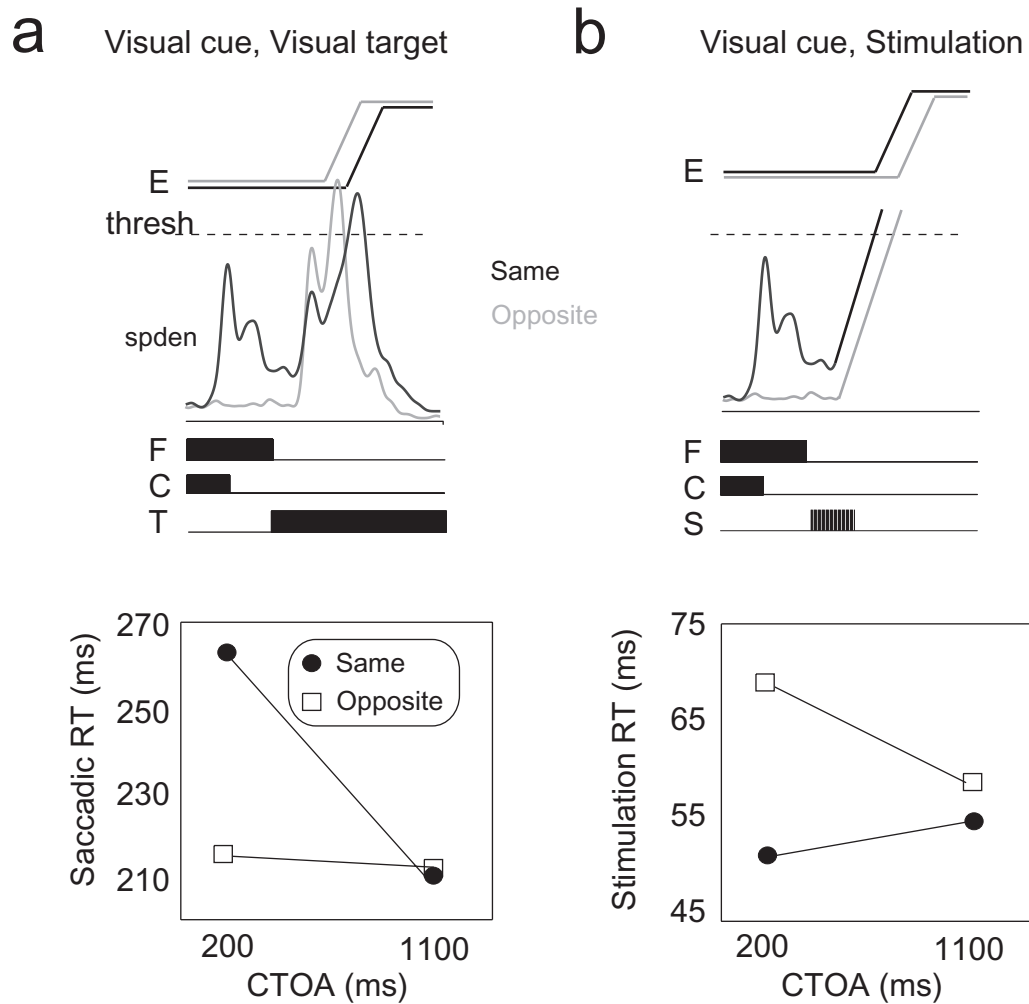


FIGURE 64.3 a. *Top*. Representative example of a single neuron when a visual target drives the saccadic response. Illustration shows that a theoretical saccadic threshold (dotted line) is achieved sooner when the cue appeared at the opposite location. b. Hypothetical example of what may happen when electrical microstimulation is applied to the SC instead of presenting a visual target, in which elevated excitability leads to saccadic threshold being achieved sooner. *Bottom*. Saccadic reaction times obtained when a visual target guided the response (left) and when microstimulation drove the response (right).

SC that show strong attenuation of the target-related response. Therefore, it is quite possible that presentation of an auditory cue will not alter the neural activity linked to the visual target for inhibition of return.

Recently, we have confirmed this hypothesis (Bell et al., 2004). Using a cue-target paradigm to contrast the consequences of auditory and visual cues on a visual target, auditory cues did not modify the behavior of the monkeys and did not alter the peak target-related activity of sensorimotor neurons in the SC.

All told, both the capture of attention and inhibition of return are associated with changes in a sensory signal or the neural salience of the target—stronger

target-related activity is linked to the capture of attention and weaker target-related activity is linked to inhibition of return (see also Chapter 36).

What do these findings mean for our understanding of the reflexive orienting of spatial attention?

Attention describes a phenomenological experience (James, 1890)—the spotlight that illuminates (brings to awareness) items that are within its beam (Posner, 1980). By many accounts, spatial attention is a stand-alone cognitive ability (e.g., Bisley and Goldberg, 2003; Colby and Goldberg, 1999; Posner, 1980; Posner and diGirolamo, 2000 (see Chapter 22). Strong support for this claim comes from the consistency with which attentional phenomena are observed across different

task manipulations—in particular, the apparent independence of attentional phenomena from the effector (hand versus eye) used to respond (Posner and diGirolamo, 2000 (see Chapter 22).

With regard to the capture of attention and inhibition of return, careful scrutiny of the role of effector shows important *inconsistencies* when hand and eye responses are compared, though. For one, the crossover from the capture of attention to inhibition of return occurs sooner when a saccade is initiated to the locus of the target than when a manual button press is used instead (Briand et al., 2000). A more dramatic difference is obtained when retinotopic and environmental spatial reference frames are dissociated with a smooth pursuit eye movement (Abrams and Pratt, 2000). In this case, inhibition of return is encoded in an environmental reference frame for manual responses, but in a retinotopic reference frame for saccadic responses. Taken together, these findings suggest that both the capture of attention and inhibition of return are represented differently in the manual and oculomotor neural networks.

Showing that the capture of attention and inhibition of return link to changes in a visual signal makes it easy to explain how these biases appear to influence a single attentional network in most instances, but change with the effector used to respond in others. In the dorsal visual pathway, visual information is used to guide action (Milner and Goodale, 1995). Changes in the strength, or salience, of this visual signal will change how efficiently or quickly it can be translated into motor acts. This would produce the changes in reaction times that we associate with the capture of attention and inhibition of return. The widespread distribution of visual information explains the congruity associated with the capture of attention and inhibition of return in most studies. However, because different networks use this information to generate a response explains the important differences that have been observed across effectors. For instance, visual information is encoded in different coordinate frames for different effectors (Colby and Goldberg, 1999), potentially explaining why inhibition of return is encoded in different reference frames for manual and saccadic responses (Abrams and Pratt, 2000).

This description explains how changes in the strength of a visual signal could give rise to behaviors we associate with the capture of attention and inhibition of return. Does this mean that these effects produced with the cue-target task tell us more about the processes involved in initiating actions than the reflexive orienting of spatial attention (see also Chapters 20 and 31)?

Albeit one possible interpretation, it alone cannot explain our unified percept of the spotlight. For instance, our phenomenological experience of the capture of attention does not feel more fleeting when responding with the eye than with the hand. (Indeed, our phenomenological experiences can be dissociated from the actions we produce altogether. See Castiello et al., 1991; Kramer et al., 2000.) If similar visual signals are distributed widely across the brain, this information will produce different consequences depending on the network(s) expressing and using this information. Perhaps, in addition to gaining access to saccadic and manual systems that produce the required response, this visual information may modify the neural processes that give rise to the phenomenological experience of the spotlight as well. Of course the future may favor another interpretation. Nonetheless, the accumulated evidence to date casts doubt on the view that these reflexive biases in orienting attention originate from and/or influence only one attentional network in the brain.

References

- Abrams, R. A., and Pratt, J. (2000). Oculocentric coding of inhibited eye movements to recently attended locations. *J. Exp. Psychol. Hum. Percept. and Perform.* **26**, 776–88.
- Andersen, R. A., Asanuma, C., Essick, G., and Siegel, R. M. (1990). Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. *J. Comp. Neurol.* **296**, 65–113.
- Basso, M., and Wurtz, R. (1997). Modulation of neural activity by target uncertainty. *Nature* **389**, 66–69.
- Bell, A. H., Corneil, B. D., Meredith, M. A., and Munoz, D. P. (2001). The influence of stimulus properties on multisensory processing in the awake primate superior colliculus. *Can. J. Exp. Psychol.*, **55**, 125–134.
- Bell, A. H., Fecteau, J. H., and Munoz, D. P. (1994) Using auditory and visual stimuli to investigate the behavioral and neuronal consequences of reflexive covert orienting. *J. Neurophysiol.* **91**, 2172–2184.
- Bisley, J. W., and Goldberg, M. E. (1998). Neuronal activity in the lateral intraparietal area and spatial attention. *Science* **299**, 54–56.
- Briand, K. A., Larrison, A. L., and Sereno, A. B. (2000). Inhibition of return in manual and saccadic response systems. *Percept Psychophys* **62**, 1512–1524.
- Castiello, U., Paulignan, Y., and Jeannerod, M. (1991). Temporal dissociation of motor responses and subjective awareness. A study in normal subjects. *Brain* **114**, 2639–2655.
- Colby, C. L., and Goldberg, M. E. (1999). Space and attention in parietal cortex. *Ann. Rev. Neurosci.* **22**, 319–349.
- Constandtinidis, C., and Steinmetz, M. A. (2001). Neuronal responses in area 7a to multiple stimulus displays: II. responses are suppressed at the cued location. *Cereb. Cortex.* **11**, 592–597.
- Dorris, M. C., and Munoz, D. P. (1998). Saccadic probability influences motor preparation signals and time to saccadic initiation. *J. Neurosci.* **18**, 7015–7026.
- Dorris, M. C., Klein, R. M., Everling, S., and Munoz, D. P. (2002). Contribution of the primate superior colliculus to inhibition of return. *J. Cog. Neurosci* **14**, 1256–1263.

- Fecteau, J. H., Bell, A. H., and Munoz, D. P. (2004). Neural correlates of the automatic and goal-driven biases in orienting spatial attention. *J Neurophysiol.* **92**, 1728–1737.
- Fecteau, J. H., and Munoz, D. P. (in submission) Correlates of capture of attention and inhibition of return across stages of visual processing.
- Glimcher, P. W., and Sparks, D. L. (1992). Movement selection in advance of action in the superior colliculus. *Nature* **355**, 542–545.
- Goodale and Milner. (1995). *A Visual Brain in Action*. Oxford: Oxford University Press.
- Gottlieb, J., Kusunoki, M., and Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature* **391**, 481–484.
- James, W. (1890). *The Principles of Psychology*. In C.D. Green, *Classics in the History of Psychology*.
<http://psychclassics.asu.edu/James/Principles/index.htm>.
- Jonides, J. (1981). Voluntary vs. Automatic control over the mind's eye's movement. In J. B. Long and A. D. Baddeley (Eds.) *Attention and Performance IX*. Lawrence Erlbaum Associates, Hillsdale, NJ.
- Kramer, A. F., Hahn, S., Irwin, D. E., Theeuwes, J. (2000) Age differences in the control of looking behavior: do you know where your eyes have been? *Psychol. Sci.* **11**, 210–217.
- Lui, F., Gregory, K. M., Blanks, R. H., Giolli, R. A. (1995). Projections from visual areas of the cerebral cortex to pretectal nuclear complex, terminal accessory optic nuclei, and superior colliculus in macaque monkey. *J. Comp. Neurol.* **363**, 439–460.
- Munoz, D. P., Dorris, M. C., Paré, M., Everling, S. (2000). On your mark, get set: brainstem circuitry underlying saccadic initiation. *Can. J. Physiol. Pharmacol.* **78**, 934–944.
- Munoz, D. P., and Fecteau, J. H. (2002). Vying for dominance: Dynamic interactions control visual fixation and saccadic initiation in the superior colliculus. *Prog. Brain Res.* **140**, 3–19.
- Pollack, J. G., and Hickey, T. L. (1979). The distribution of retinocollicular axon terminals in rhesus monkey. *J. Comp. Neurol.* **185**, 587–602.
- Posner, M. I., and Cohen, Y. (1984). Components of visual orienting. In H. Bouma and D. G. Bouwhuis (Eds.), *Attention and performance X* (pp. 531–556). Erlbaum Hillsdale, NJ.
- Posner, M. I. (1980). Orienting of spatial attention. *Quarterly Journal of experimental Psychology* **32**, 2–27.
- Posner, M. I., Rafal, R. D., Choate, L. S., and Vaughan, J. (1985). Inhibition of return: neural basis and function. *Cog. Neuropsychology* **2**, 211–228.
- Posner, M. I., and diGirolamo, G. J. (2000). Attention in Cognitive Neuroscience: An Overview. In *The New Cognitive Neurosciences, 2nd ed.*, M. S. Gazzaniga, ed., 623–631. MIT Press, USA.
- Robinson, D. L., Bowman, E. M., and Kertzman, C. (1995). Covert orienting of attention in macaques. II. Contributions of the parietal cortex. *J. Neurophys.* **74**, 698–712.
- Sapir, A., Soroker, N., Berger, A., and Henik, A. (1999). Inhibition of return in spatial attention: direct evidence for collicular generation. *Nat. Neurosci.* **2**, 1053–1054.
- Steinmetz, M. A., Connor, C. E., Constantinidis, C., and McLaughlin, J. R. (1994). Covert attention suppresses neuronal responses in area 7a of the the posterior parietal cortex. *J. Neurophysiol.* **72**, 1020–1023.
- Wallace, M. T., Wilkinson, L. K., and Stein, B. E. (1996). Representation and integration of multiple sensory inputs in primate superior colliculus. *J. Neurophysiol.* **76**, 1246–1266.