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Control from below: the role of a midbrain network in spatial attention

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Abstract

Spatial attention enables the brain to analyze and evaluate information selectively from a specific location in space, a capacity essential for any animal to behave adaptively in a complex world. We usually think of spatial attention as being controlled by a fronto-parietal network in the forebrain. However, emerging evidence shows that a midbrain network also plays a critical role in controlling spatial attention. Moreover, the highly differentiated, retinotopic organization of the midbrain network, especially in birds, makes it amenable to detailed analysis with modern techniques that can elucidate circuit, cellular and synaptic mechanisms of attention. The following review discusses the role of the midbrain network in controlling attention, the neural circuits that support this role, and current knowledge about the computations performed by these circuits.

Keywords

Superior colliculus; optic tectum; stimulus selection; working memory; birds

Introduction

Operating beneath the forebrain is a midbrain network that exerts an astonishing degree of control over attention. The midbrain network interacts directly and indirectly, via the thalamus, with the well-known fronto-parietal network in the forebrain to control the locus of attention (Boehnke & Munoz, 2008). The network comprises four major components. One component is located in the superficial layers of the superior colliculus (SC, called the optic tectum, OT, in non-mammalian vertebrates) and contains a topographic map of the locations of salient visual stimuli (Goldberg & Wurtz, 1972b). Another component, in the deeper, multimodal and motor layers of the SC/OT, contains a space map that prioritizes locations based on the multimodal salience of stimuli, the behavioral relevance of those stimuli, and goals of planned orienting movements (Fecteau & Munoz, 2006). A third component consists of specialized cholinergic and GABAergic circuits, formed by the isthmus nuclei, that appear to mediate spatially selective enhancement and global competitive interactions within the network (Wang, 2003; Wang et al., 2006). A fourth component consists of the substantia nigra (Hikosaka & Wurtz, 1985b; Comoli *et al.*, 2003), which gates commands for orienting movements from the network (substantia nigra pars reticulata) and signals the occurrence of important events to the forebrain (substantia nigra pars compacta). This review discusses the role that this network plays in selecting the most important stimulus among multiple stimuli at each moment in time. Because the contribution of the substantia nigra to this process is not known, it will not be discussed further in this review.

The basic midbrain network exists in all vertebrate animals from fish to mammals (Fig. 1) (Luiten, 1981; Wang, 2003; Gruberg *et al.*, 2006). Its role in orienting gaze toward stimuli in the environment is well established in all classes of vertebrates (Stein & Meredith, 1993). However, its role in selecting stimuli for attention has been demonstrated only in monkeys (McPeck & Keller, 2004; Lovejoy & Krauzlis, 2010). Nevertheless, since all vertebrate species must be capable of selectively processing information that is most relevant to behavior, the preservation of this network across hundreds of millions of years of evolution suggests that it provides a solution to competitive stimulus selection that is required by all vertebrate species. Despite differences in aspects of the network that reflect differences in the cognitive capacities and vast evolutionary distances of species, accumulating evidence indicates that it contains fundamental circuits and mechanisms for competitive stimulus selection that have been conserved across evolution.

Unless otherwise noted, the statements in this review refer to data from mammals and birds. The vast majority of what we know about the functional properties of the midbrain network comes from studies of behaving mammals, particularly monkeys. The advantage of monkeys is the ability to characterize the functional properties of the network in animals that are performing sophisticated behavioral tasks that facilitate the identification and description of component processes of stimulus selection. Our understanding of the network's intrinsic circuitry comes primarily from studies of birds. The advantage of studying birds is that the anatomy of the network is highly differentiated and many of the component circuits are spatially segregated (Fig. 1, right).

An essential role of the midbrain network in spatial attention

The involvement of the midbrain network in controlling spatial attention has been suspected for decades based on the network's involvement in controlling gaze. Early research, beginning well over a century ago, demonstrated a role of the SC in gaze control (Adamuk, 1870). Robinson later discovered that electrical microstimulation of the SC in monkeys evokes conjugate saccadic eye movements, the magnitude and direction of which depend on the site of microstimulation in the SC. He showed that the end-points of the evoked eye movements form a topographic motor map of space in the SC that aligns with a coexisting visual map of space (Robinson, 1972). Similar results have been obtained from the SC/OT in all classes of vertebrates (Ingle, 1983; du Lac & Knudsen, 1990; Stein & Meredith, 1993). In addition, when a monkey selects a visual stimulus as the target for a shift in gaze, the responses of SC neurons with receptive fields containing the visual stimulus are enhanced (Wurtz & Mohler, 1976; Li & Basso, 2005; 2008). The inference that the SC/OT might also be involved in controlling spatial attention was based on the obligatory coupling between motor plans to change gaze direction and momentary shifts in the locus of attention, as observed in humans (Hoffman & Subramaniam, 1995; Kowler *et al.*, 1995; Deubel & Schneider, 1996) and monkeys (Moore *et al.*, 2003) and thought to exist in all vertebrate species.

The suspected involvement of the midbrain network in controlling spatial attention was supported further by extensive neurophysiological recordings from monkeys engaged in attention-demanding tasks (Goldberg & Wurtz, 1972b; Ignashchenkova *et al.*, 2004; Fecteau & Munoz, 2006). Physically salient stimuli (high intensity, moving, or novel), which automatically capture spatial attention (Posner, 1980), were found to be exceptionally powerful stimuli for driving activity in the midbrain network (Wurtz & Albano, 1980). In addition, some SC neurons increase and sustain their responses when a stimulus inside their receptive field is selected for a perceptual judgment or as a goal for future action (Wurtz & Albano, 1980; McPeck & Keller, 2002b; a; Horwitz *et al.*, 2004).

The data cited above, while highly suggestive, are correlational and inferential. However, recent experiments in monkeys demonstrate clear, causal roles for the midbrain network in target selection and the control of spatial attention. Reversible inactivation of a portion of the SC on one side dramatically reduces the probability that a monkey will select, from a group of stimuli, an oddball stimulus (based on color or luminance) as the target for a gaze shift when that stimulus is represented in the inactivated portion of the SC space map (McPeck & Keller, 2004). The impairment in target selection caused by SC inactivation increases dramatically when the difference between the oddball stimulus and the competing stimuli in the array is difficult to detect. In contrast, selection of the oddball stimulus when presented alone is not impaired. Thus, the contribution of the SC to stimulus selection is essential when a monkey must select among similarly salient, competing stimuli.

In other experiments, weak electrical microstimulation of the SC has been shown to increase the likelihood that a monkey will select a stimulus at the location represented by the site of microstimulation (Carello & Krauzlis, 2004). Monkeys were trained to select a cued stimulus, out of a pair of stimuli, for either a pursuit or a saccadic eye movement. When either stimulus (cued or non-cued) was at the location represented by the microstimulation site, the probability that the monkey would select that stimulus increased.

Other electrical microstimulation experiments demonstrated that focal SC activation can act, in place of a salient cue, to shift attention to a particular location (Cavanaugh & Wurtz, 2004; Muller *et al.*, 2005). Monkeys improved their perceptual judgments of visual motion direction and changes in motion direction specifically for stimuli at the location represented at the microstimulation site. Since the SC is not organized systematically according to visual motion direction, microstimulation could not have enhanced a directional signal in the SC itself. Instead, the results suggest that microstimulation causes the SC to issue a space-specific signal that enhances the processing of motion direction information, presumably in the forebrain network and, perhaps, in area MT (Rodman *et al.*, 1989; Berman & Wurtz, 2008).

Finally, focal inactivation of the SC has revealed a role of the SC in sustaining voluntary attention at a particular location in space (Lovejoy & Krauzlis, 2010). Monkeys were trained to report the direction of coherent motion of a cued, random dot stimulus (Fig. 2A, red ring) and to ignore the direction of an orthogonally moving, but otherwise identical, random dot stimulus (task-relevant distracter or foil; Fig. 2A, dots near yellow arrow) presented simultaneously at another location (Fig. 2B). When the cued stimulus was at a location represented in the inactivated portion of the SC, the monkey reported the direction of the foil stimulus, rather than the direction of the cued stimulus, as though it were unable to maintain attention on the cued stimulus (Fig. 2C–E). However, the monkey reported the direction of the cued stimulus correctly even when it was in the inactivated portion of the visual field, when either the foil was absent or was replaced by a task-irrelevant stimulus. Thus, the critical contribution of the SC to sustaining the locus of attention is revealed specifically in the context of competition among similar, task-relevant distracters.

A recurring theme from these behavioral experiments is the critical importance of the midbrain network in stimulus selection or in sustaining the locus of attention, when competing stimuli are similarly salient. The results suggest that the midbrain network is required for comparing the relative properties of competing stimuli and selecting the one with highest priority for attention. The following sections discuss our current knowledge of the circuits and response properties in the midbrain network that may underlie these functions.

In the following sections, three key components of the midbrain network are described, each component having distinct inputs and outputs, intrinsic circuitries, and functions. The three components are the visual layers of the SC (SCv), or OT (OTv) in non-mammals, the multimodal and motor layers of the SC/OT (SCm/OTm), and the isthmic nuclei (Fig. 1).

The visual layers of the SC/OT: the SCv/OTv

The SCv/OTv has inputs and outputs that link it tightly with structures that analyze visual information (Fig. 3). In both mammals and birds, the SCv/OTv receives direct input from the retina, as well as inputs from visual forebrain areas: from the striate and extrastriate visual cortex in mammals (Wurtz & Albano, 1980; Boehnke & Munoz, 2008) and from the visual hyperpallium in birds (Karten *et al.*, 1973). The outputs of the SCv/OTv project to visual processing structures in the brainstem and thalamus. In mammals, these include the lateral geniculate nucleus (LGN) and the inferior Pulvinar (PULi), nuclei that connect with striate and extrastriate visual cortical areas that analyze visual features (Kaas & Lyon, 2007; Berman & Wurtz, 2008; Boehnke & Munoz, 2008). In birds, these outputs include projections to the LGN (Reiner & Karten, 1982; Wild, 1989; Hu *et al.*, 2004), which connects with the visual hyperpallium, a forebrain structure that analyses visual features (Pettigrew & Konishi, 1976; Nieder & Wagner, 1999; 2001), and to the isthmo-optic nucleus (ION) (Uchiyama & Watanabe, 1985; Miceli *et al.*, 1997), which modulates visual responses in the retina itself (Reperant *et al.*, 2006).

In mammals, the SCv comprises the upper 3 layers of the SC (Fig. 1, left). The SCv is typically referred to as the superficial layers or SCs. This review uses its functional designation (SCv) because the comparisons made across vertebrate classes are based on functional, not anatomical, criteria. The boundary between the SCv and the SCm is demarcated clearly by the stratum opticum, which contains the afferent axons from the retina.

In birds, the circuits of the OTv and OTm overlap in layer 10 (Fig. 1, right). Retinal axons enter the OT through the most superficial lamina, layer 1, and arborize in layers 3, 4, 5 and 7 (Yamagata & Sanes, 1995). Descending visual input from the hyperpallium in the forebrain, projects to essentially all layers of the OT (Karten *et al.*, 1973; Miceli *et al.*, 1987). Inputs from auditory structures in the brainstem (Hyde & Knudsen, 2000) and inputs from motor regions of the forebrain project to layers 10–15 (Knudsen *et al.*, 1995). Some neurons in layer 10 function as part of the OTv: they receive retinal and visual forebrain input and they project to the LGN or to the ION (Wild, 1989; Miceli *et al.*, 1997). However other neurons, in the lower portion of layer 10, extend dendrites both into the retino-recipient layers and down into the multimodal and motor layers of the OT (Fig. 4) (Wang *et al.*, 2004). These neurons send axons to the isthmus nuclei, a component of the midbrain network that is involved with competitive stimulus selection (discussed below) and to auditory nuclei in the brainstem (Hyde & Knudsen, 2000). These layer 10 neurons function as part of the OTm. Thus, layer 10 contains some neurons that contribute to the OTv as well as others that contribute to the OTm.

Neural activity in the SCv/OTv represents the locations of salient visual stimuli (Goldberg & Wurtz, 1972b; Jassik-Gerschenfeld & Guichard, 1972; Hughes & Pearlman, 1974; Woods & Frost, 1977; Wurtz & Albano, 1980). Neurons in the SCv/OTv have relatively small spatial receptive fields and are organized into a topographic map of the contralateral retina or, in primates, of contralateral visual space (Lane *et al.*, 1973). Nearly all neurons in the SCv/OTv respond to contrast and motion, with higher responses to greater contrasts and speeds (greater physical salience). However, unlike in forebrain visual pathways, there is no evidence that values of features (e.g., contour orientation, speed or color) are analyzed in the SCv/OTv. Although some SCv/OTv neurons exhibit preferences for motion direction or

contour orientation (Goldberg & Wurtz, 1972a; Frost & DiFranco, 1976; Wurtz & Albano, 1980), these preferences are weaker and less pervasive than those observed in forebrain visual areas, which project to the SCv/OTv, or even than those observed in the retina (Olveczky *et al.*, 2003; Gollisch & Meister, 2010). Preferences that are expressed for feature values may depend on descending input from the visual cortex, at least in mammals (Wickelgren & Sterling, 1969). There is also no evidence of functional organization within the SCv/OTv according to any visual feature, except stimulus location. In addition, neurons in the SCv/OTv habituate to stimuli that are repeated and are not behaviorally relevant (Cynader & Berman, 1972; Goldberg & Wurtz, 1972a; Hughes & Pearlman, 1974; Woods & Frost, 1977; Kohn, 2007). These functional properties indicate that the SCv/OTv does not analyze visual features but, instead, combines information across features and feature values to represent the locations of physically salient visual stimuli.

There is no evidence that non-visual sensory input drives responses in the SCv/OTv. However, inputs from other sensory modalities might modulate visually driven activity. In owls, potentially modulatory auditory input reaches the OTv by way of the cholinergic isthmus circuit (Fig. 4, red) (Maczko *et al.*, 2006; Wang *et al.*, 2006). The neurons in this circuit generate large amplitude, axonal spikes that are recorded throughout the OTv (Knudsen, 1982; Marin *et al.*, 2005). This auditory activity originates in OT layer 10, which represents the uppermost multimodal layer in the bird OT (Fig. 1, right) and which contains the neurons that provide input to the isthmus circuits (Fig. 4). However, multimodal modulation of somatic spike responses in the OTv (or in the SCv) has yet to be demonstrated.

Neuronal activity in the SCv is also not driven in association with eye movements, as shown by electrophysiological recordings in monkeys making orienting eye saccades (Goldberg & Wurtz, 1972b). However, plans to make an eye saccade modulate visually driven activity in the SCv powerfully (Wurtz & Mohler, 1976; Dunn *et al.*, 2010). The responses of SCv neurons to a visual stimulus inside the classical receptive field are enhanced when a monkey plans to make an eye saccade to a location in or near the neuron's classical receptive field. This enhancement could be due, in part, to input from cholinergic neurons in the isthmus complex that project heavily to the SCv (Graybiel, 1978) and which contain neurons that discharge in association with eye movements (Cui & Malpeli, 2003). The modulation of visual responses by movement-related inputs, and possibly by multisensory inputs, indicates that the SCv/OTv represents more than just the physical visual salience of stimuli.

The SCv/OTv transmits a high spatial-resolution, retinotopic representation of the locations of salient visual stimuli to the forebrain (Reiner & Karten, 1982; Boehnke & Munoz, 2008) and, in birds, to the retina itself via the ION (Fig. 3) (Reperant *et al.*, 2006). These pathways have the capacity to enhance responses in retinotopically organized, visual forebrain areas in a space-specific (but not feature-specific) manner, and could act as a spatial "spotlight" to reduce thresholds and increase response gains and resolution in the forebrain areas (Luck *et al.*, 1997; Reynolds & Chelazzi, 2004; Shipp, 2004; Maunsell & Treue, 2006; Marin *et al.*, 2007). This pathway could contribute, for example, to the improvement in motion perception in monkeys that results from electrical microstimulation of the SC (Muller *et al.*, 2005).

The multimodal and motor layers of the SC/OT: the SCm/OTm

The multimodal and motor layers of the SC/OT (SCm/OTm) constitute a second component of the midbrain network (Fig. 1, purple). This component serves a wider range of functions than does the SCv/OTv. In mammals, the SCm consists of the lower 4 layers of the SC (Fig. 1, left), typically referred to as the deep or intermediate and deep layers (SCid; the functional designation SCm will be used in this review). In birds, the OTm consists of layers

10–15 (Fig. 1, right). Major sensory inputs to the SCm/OTm (visual, auditory and somatosensory) originate in sensory areas in the forebrain and brainstem (Fig. 3)(Karten *et al.*, 1973; Wurtz & Albano, 1980; Knudsen & Knudsen, 1983; Stein & Meredith, 1993; King *et al.*, 1998). Major movement related inputs originate from gaze control areas of the forebrain, from the frontal eye field (FEF) in mammals (Stanton *et al.*, 1988) and from the arcopallial gaze field (AGF) in birds (Knudsen *et al.*, 1995; Manns *et al.*, 2007), and from the substantia nigra pars reticulata in mammals and birds (Reiner *et al.*, 1984; Hikosaka & Wurtz, 1985a). In mammals, additional inputs originate in the lateral intraparietal area (LIP) and in the dorsolateral prefrontal cortex (DLPFC) (Lynch *et al.*, 1985; Johnston & Everling, 2006).

Sensory responses in the SCm/OTm merge information about the physical salience of stimuli with information about the behavioral relevance of those stimuli (Fecteau & Munoz, 2006; Winkowski & Knudsen, 2007). Sensory inputs to the SCm/OTm provide multimodal information about the locations of salient stimuli (Stein & Meredith, 1993; Bell *et al.*, 2005). Receptive fields are larger in the SCm/OTm than in the SCv/OTv (Hughes & Pearlman, 1974; Woods & Frost, 1977; Wurtz & Albano, 1980). Nevertheless, they are organized to form a retinotopic map of space that aligns with the space map in the SCv/OTv. Some neurons are selective for one sensory modality or another (Cotter, 1976; Knudsen, 1982; Stein & Meredith, 1993), or even for one stimulus feature, e.g., visual motion (Frost & DiFranco, 1976; Luksch *et al.*, 2001). However, as in the SCv/OTv, neurons in the SCm/OTm are rarely selective for particular values of features (e.g., direction or speed), there is no organization according to sensory feature value (Wurtz & Albano, 1980), and responses increase in strength with increasing strength of physically salient features, such as stimulus intensity or motion speed (Knudsen, 1984; Li & Basso, 2008; Mysore *et al.*, 2010). As a result, across populations of SCm/OTm neurons, stimulus-driven responses provide a modality-independent, topographic representation of the locations of physically salient stimuli.

The responses of SCm neurons to a physically salient stimulus can be modulated strongly by the behavioral relevance of the stimulus. The behavioral relevance of a stimulus may be based on innate predispositions of the species or be learned as a result of the individual's own experience (Horwitz *et al.*, 2004; Fecteau & Munoz, 2006). In addition, the behavioral relevance of a stimulus can vary in real-time as a consequence of the animal selecting the stimulus for attention, particularly when the animal plans to orient its gaze toward the stimulus (Goldberg & Wurtz, 1972b). Inputs that convey information about the behavioral relevance of a stimulus originate from forebrain structures such as the DLPFC, LIP, FEF and visual cortex (Fig. 3)(Sommer & Wurtz, 2000; Thompson & Bichot, 2005; Johnston & Everling, 2006; Bisley & Goldberg, 2010). The circuitry in the SCm integrates this information with information about the physical salience of stimuli to produce a retinotopic representation of the relative priorities of different locations as the next locus for spatial attention and gaze (Fecteau & Munoz, 2006; Dorris *et al.*, 2007; Shen & Pare, 2007; Mysore *et al.*, in press).

In mammals, the SCm sends information back up to the parietal and prefrontal forebrain areas via the dorsal pulvinar (PULd) and anterior thalamus (Fig. 3)(Shipp, 2004; Kaas & Lyon, 2007; Boehnke & Munoz, 2008). This closes feedback loops with the LIP and FEF. According to one model, a gaze shift is initiated when the cumulative activity of movement-related neurons in the SCm (midbrain network) and the FEF (forebrain network) reaches some threshold level at a particular location in the space map (Munoz & Schall, 2003). An analogous proposal could apply to shifts in spatial attention: a shift in spatial attention occurs when the cumulative activity of sensory-related neurons in the SCm, LIP and FEF reaches a threshold level. Consistent with this proposal, electrical microstimulation of either

the SC or the FEF shifts a monkey's attention to the location represented at the microstimulation site (Moore & Fallah, 2004; Muller *et al.*, 2005). Reverberant interactions between the SCm, in the midbrain network, and the DLPFC, LIP and FEF, in the forebrain network, may also be necessary for sustaining spatial attention at a particular location, and could account for the impaired ability of monkeys to sustain attention at a location when the SC, LIP or FEF is inactivated (Wardak *et al.*, 2004; Wardak *et al.*, 2006; Lovejoy & Krauzlis, 2010).

In birds, the OTm transmits information to the entopallium (Reches & Gutfreund, 2009; Reches *et al.*, 2010) via the thalamic nucleus rotundus (ROT; Fig. 3). It is possible that portions of these structures act in a manner that is functionally analogous to the mammalian LIP and PULd, respectively. However, unlike in mammals, the bird OTm also projects heavily to visual feature selective regions in the ROT (Wang *et al.*, 1993; Gunturkun & Hahmann, 1999; Hellmann & Gunturkun, 2001; Wylie *et al.*, 2009). This projection is functionally analogous to the projections of the mammalian SCv to the PULi, discussed earlier (Fig.3), that modulate feature selective visual areas in the extrastriate visual cortex (Karten *et al.*, 1997; Kaas & Lyon, 2007). Thus, in birds, the relative priority information that is represented in the OTm appears to modulate visual feature processing in the forebrain directly. In contrast, in mammals, priority information from the SCm reaches extrastriate, visual feature processing areas indirectly, via the LIP and FEF in the forebrain network (Bisley & Goldberg, 2010).

Stimulus prioritization in the SCm/OTm—The behavioral deficits that result from inactivation of the SC in monkeys (e.g., Fig. 2) demonstrate that, under many conditions, the essential contribution of the SC to attention control is in selecting among similarly salient stimuli (McPeck & Keller, 2004; Lovejoy & Krauzlis, 2010). This essential contribution implies that the midbrain network compares the priorities of stimuli across space and is necessary for computing the relative priorities of those stimuli, especially when they are similarly salient. Evidence of both capacities has been reported in the SCm/OTm. Strong competitive interactions between the representations of widely separated stimuli have been observed in numerous species (Rizzolatti *et al.*, 1974; Schellart *et al.*, 1979; Munoz & Istvan, 1998; Mysore *et al.*, 2010). For a large proportion of SCm/OTm neurons, responses to a stimulus inside the classical receptive field are suppressed, sometimes completely, by another stimulus (of the same or different sensory modality) presented simultaneously at a distant location (Fig. 5). The competitive fields of many neurons have been shown to extend across the entire visual field, although competitive interactions are much stronger when stimuli are located within the same visual hemifield (Mysore *et al.*, 2010).

In addition, a subset of OTm neurons exhibit a specialized capacity to discriminate among similarly salient stimuli (Mysore *et al.*, in press). About 30% of OTm neurons in owls exhibit highly unusual competitive interactions when a passive, untrained animal is confronted with pairs of stimuli (Fig. 6). When the strength of an effective stimulus inside a neuron's receptive field is held constant and the strength of a distant competing stimulus is gradually increased, these neurons switch abruptly from responding strongly to responding more weakly when the competing stimulus becomes the stronger stimulus (Fig. 6C; data to the right of the black arrowhead). The activity of these "switch-like" neurons creates a categorical representation in the OTm of the location of the strongest (highest priority) stimulus. The abruptness of the switch from strong to weaker responses, just when a competing stimulus becomes the stronger stimulus, indicates that these neurons discriminate finely between the relative excitatory drives associated with similarly salient, competing stimuli. Neurons with such high-resolution, competitive properties could account for the essential contribution of the SC to discriminating among similarly salient, competing stimuli that has been observed in behaving monkeys.

In the SCm of monkeys, stimulus-driven responses are modulated by descending inputs from the forebrain network, depending on the behavioral relevance of the stimulus, (Fecteau & Munoz, 2006). The sensory responses of OTm neurons in the owl also incorporate top-down influences in their representation of stimuli (Fig. 7)(Winkowski & Knudsen, 2007; 2008). The forebrain gaze field, the AGF, provides spatial working memory information to the gaze control system (Knudsen & Knudsen, 1996). Strong electrical microstimulation applied to the AGF causes owls to make a saccadic shift of gaze direction (Knudsen et al., 1995). Weak electrical microstimulation causes no shift in gaze but, instead, enhances the representation of sensory stimuli in the OTm space map, specifically for stimuli at the location represented by the AGF microstimulation site (Fig. 7B), an effect that is remarkably similar to the effect of microstimulating the FEF on responses in the extrastriate visual cortex in monkeys (Armstrong *et al.*, 2006; Armstrong & Moore, 2007). At the same time, AGF microstimulation decreases the stimulus-driven responses of OTm neurons representing stimuli at all other locations (Fig. 7C). In the context of stimulus prioritization, this top-down modulatory influence should increase the priority of stimuli specifically at the location represented by the AGF signal.

The isthmic nuclei

A third component of the midbrain network consists of a cluster of specialized cholinergic, glutamatergic and GABAergic neurons, lying just beneath the SC/OT, that interconnect extensively with the SC/OT (Figs. 1 and 7). These neurons are referred to collectively as the isthmic nuclei (Serenio & Ulinski, 1987; Wang, 2003; Gruberg *et al.*, 2006). The isthmic nuclei are most highly differentiated in birds, although they are conspicuous in all classes of vertebrate animals. In birds, sub-types of cholinergic neurons are separated into adjacent nuclei: the nucleus isthmi pars parvocellularis (Ipc) and the smaller, nucleus semilunaris (SLu)(Hellmann et al., 2001; Wang et al., 2006); the SLu also contains neurons that project to the ROT in the thalamus. The disseminated nucleus (ID; Fig. 1, right) is a glutamatergic nucleus that receives input from the ipsilateral OT and projects predominantly to the OT on the contralateral side (unpublished observations in barn owls). The nucleus isthmi pars magnocellularis (Imc) contains GABAergic neurons (Wang et al., 2004). In mammals, the organization of the different kinds of isthmic neurons is less differentiated but conspicuous nonetheless, with cholinergic neurons and the neurons projecting to the contralateral SC and to the PUL in the thalamus clustered in the parabrachial nucleus (PBN; Fig. 1, left) (Wang, 2003; Motts et al., 2008) and the GABAergic neurons clustered in the peribrachial nucleus (LTN) (Graybiel, 1978; Appell & Behan, 1990; Jiang *et al.*, 1996).

The circuitry of the isthmic nuclei exhibits a geometry (particularly well differentiated in birds) that strongly suggests its role both in spatially selective response enhancement and in global competitive interactions within the midbrain network (Wang et al., 2004; Wang et al., 2006). In birds, each of the isthmic nuclei receives a topographic projection from neurons in layer 10 of the OTm (Fig. 4, purple), although the topography of the projection is more precise to the cholinergic nuclei than to the GABAergic nucleus. Each nucleus projects back to the OT: the cholinergic neurons (Fig. 4, red) project focally and topographically to the OTv and OTm, and the GABAergic neurons (Fig. 4, green) project broadly across the space map in the OTm.

The cholinergic circuit—The pattern of connections between the isthmic cholinergic neurons and the SC/OT (Fig. 4A, purple and red) suggests a role of this circuit in the space-specific enhancement of information processing in the SC/OT. A major fraction of the PBN/Ipc input to the SC/OT terminates in the retinal recipient, superficial layers (Graybiel, 1978; Wang et al., 2006). Axon terminals of retinal ganglion cell afferents express presynaptic, nicotinic cholinergic receptors (Prusky & Cynader, 1988; King, 1990; Titmus *et al.*, 1999).

Nicotinic agonists increase responses in the SCv/OTv evoked by either visual stimuli or by optic nerve stimulation, and nicotinic antagonists decrease these evoked responses (Edwards & Cline, 1999; Binns & Salt, 2000). In goldfish, microstimulation of the isthmic nuclei enhances responses in the OT evoked by optic tract stimulation, and this enhancement is blocked by nicotinic antagonists (King & Schmidt, 1991). In addition, inhibitory interneurons within the SCv/OTv and SCm/OTm express nicotinic and/or muscarinic receptors (Lee et al., 2001; Endo et al., 2005). Thus, the cholinergic isthmic circuit has the capacity to increase the sensitivity of SCv/OTv and SCm/OTm neurons to visual input, at least in part through presynaptic facilitation of glutamate release from retinal ganglion cell axons and, simultaneously, to sharpen spatial tuning, by activation of local, laterally inhibitory interneurons in the SC/OT.

The response properties of neurons in these cholinergic nuclei (Sherk, 1979; Cui & Malpeli, 2003; Maczko *et al.*, 2006) reflect those of neurons in the SCm/OTm, from which they derive their input (Baleydier & Magnin, 1979; Wang *et al.*, 2006). Neurons in the PBN and the Ipc respond strongly to motion, but are not selective for stimulus features, and receptive fields are organized in a retinotopic space map. In the owl, Ipc neurons are multimodal, with mutually aligned auditory and visual spatial receptive fields (Maczko *et al.*, 2006). Most importantly, however, Ipc neurons signal the relative strengths of competing stimuli (Asadollahi et al., 2010). The responses of neurons in the owl Ipc to a stimulus centered in the receptive field can be suppressed by a second, distant stimulus (auditory or visual) located at any other location outside of the neuron's classical receptive field (Fig. 8A). For about a third of the neurons, this global competition acts in a switch-like manner, as it does for a subset of neurons in the OTm (Fig. 6). These switch-like Ipc neurons respond briskly when the stimulus inside the receptive field is the stronger stimulus and more weakly when the competing stimulus is the stronger stimulus (Fig. 8A). As a result, this isthmic circuit sends a space-specific input to both the OTv and the OTm that strongly favors the representation of the stronger stimulus.

In addition, Ipc neurons respond to stimuli with periodic (25–50 Hz) bursts of spikes, a frequency of periodic firing that is referred to as the “low gamma range” (Fig. 8B,C). Gamma oscillations of the local field potential in the OT have been observed in response to sensory stimulation (Neuenschwander & Varela, 1993; Devarajan *et al.*, in press), and increases in the power of gamma oscillations in various structures of the forebrain network correlate with attention (Fries *et al.*, 2001; Buschman & Miller, 2007; Gregoriou *et al.*, 2009; Khayat *et al.*, 2010). In the midbrain network, stimulus-driven activity from the Ipc to the OT has been shown to be necessary for gating ascending activity to the thalamic nucleus ROT on the way to the forebrain network (Marin et al., 2007).

The data presented above strongly suggest that the cholinergic isthmic circuit modulates information processing in the SC/OT in a space-specific manner. During bottom-up control of stimulus selection, this cholinergic circuit could automatically enhance responses to the strongest stimulus by modulating responsiveness in both the SCv/OTv and the SCm/OTm and, during voluntary control of spatial attention, this same circuit could enhance responses to stimuli at the selected location, as instructed by top-down influences. However, direct evidence of the specific effects of this cholinergic circuit on information processing in the SCv/OTv or SCm/OTm is still lacking.

The GABAergic circuit—The GABAergic neurons in the isthmic nuclei are thought to mediate global competitive interactions in the midbrain network. This proposition is based largely on the cytoarchitecture of this circuit in turtles and birds (Sereno & Ulinski, 1987; Wang *et al.*, 2004). The GABAergic isthmic nucleus is called the nucleus isthmi pars magnocellularis (Imc) in birds (Fig. 4, green). All Imc neurons exhibit dense, somatic,

immunohistochemical staining for GABA and are, therefore, presumed to exert an inhibitory influence on their target neurons. Imc neurons receive a topographic projection predominantly from neurons in layer 10, the same layer that projects to the cholinergic isthmic nuclei (Wang et al., 2006). Imc neurons project back to the OTm to all portions of the space map, except the portion that provided input (Fig. 4). A separate population of neurons in the Imc projects broadly to the cholinergic nuclei (both to the Ipc and the SLu).

Evidence that the Imc can mediate global competitive inhibition in the midbrain network was provided by Marin et al. (2007). They measured responses in the Ipc of pigeons to sequentially presented visual stimuli that were widely separated in space (by 65°). Under normal conditions, the onset of a second stimulus suppresses Ipc responses to the first stimulus. When synaptic transmission in the Imc was blocked pharmacologically, this suppressive effect of the second stimulus on Ipc responses to the first stimulus was substantially reduced.

The two structures in the midbrain network that receive broadly projecting anatomical input from the Imc (the OTm and the Ipc; Fig. 4) also contain high proportions of neurons that exhibit strong global competitive surrounds when tested physiologically (Asadollahi et al., 2010; Mysore et al., 2010). These data suggest that the GABAergic isthmic circuit contributes to global competitive interactions within the midbrain network: It is connected optimally to suppress responses to lower priority stimuli, both directly in the OTm and, indirectly, by inhibiting the cholinergic circuit that is thought to enhance excitatory responses in both the OTv and OTm (Fig. 4).

Putative complementary effects of the isthmic circuits

The geometry and connectivity of the isthmic circuits suggest the coordinated action of two functionally complementary mechanisms in the midbrain network: a cholinergic mechanism that operates focally and a GABAergic mechanism that operates globally (Fig. 4). Experiments, in owls, in which top-down signals from the AGF were used to modulate sensory responses in the OTm, revealed effects that bear striking correspondences with the respective properties of these isthmic circuits (Winkowski & Knudsen, 2008). Weak electrical microstimulation in the AGF increases the sensitivity, responsiveness and spatial resolution of OTm neurons that have receptive fields that overlap the location represented at the AGF microstimulation site (e.g., Fig. 7B). At the same time, the response gain of OTm neurons representing stimuli at all other locations decreases (e.g., Fig. 7C).

These distinct effects of AGF microstimulation are consistent with the hypothesized actions of the isthmic nuclei. The focal enhancement of neuronal sensitivity in the OTm with AGF microstimulation (Fig. 7B) suggests the action of the spatially precise, cholinergic isthmic circuit (Fig. 4, red). The enhancement effect decreases the intensity threshold of OTm neurons (Winkowski & Knudsen, 2008). These effects are reminiscent of results from experiments in humans, demonstrating that attention decreases the intensity threshold for stimulus detection and discrimination (Yeshurun & Carrasco, 1999; Carrasco *et al.*, 2004).

The global decrease in response gain for OTm neurons representing locations other than the location represented at the AGF microstimulation site (e.g., Fig. 7C) suggests the action of the globally projecting, GABAergic isthmic circuit (Fig. 4, green). The effects of decreasing response gain are greatest for strong stimuli (Winkowski & Knudsen, 2008), reminiscent of the increasing benefit afforded by spatial attention in suppressing the effects of distracting stimuli as the strength of those stimuli increases (Pestilli & Carrasco, 2005).

Interactions between midbrain and forebrain networks

The forebrain contains its own well-known network of structures that mediate stimulus selection for gaze and attention. The network consists of the prefrontal cortex (particularly the DLPFC and the FEF), the posterior parietal cortex (particularly the LIP), the sensory areas of cortex, and the nuclei in the thalamus that interconnect these structures. Together, they filter for salient stimuli, select for the highest priority location, analyze and evaluate information from the selected location, and regulate the sensitivity and quality of sensory processing for the selected location (Fig. 9, right) (Thompson & Bichot, 2005; Bisley, 2010; Knudsen, in press). The midbrain network (Fig. 9, left) interconnects extensively with this forebrain network: it receives direct descending projections from each forebrain structure and influences each of them indirectly via ascending projections through the thalamus (Fig. 3).

The priority maps contained in the midbrain network influence different levels in this forebrain network in mammals and birds (Fig. 3). In mammals, the SCv sends a space-specific retinotopic signal, containing little or no information about feature values, to primary and secondary visual areas in the forebrain (via the LGN and PULi) that analyze feature values such as orientation, movement direction or color (Shipp, 2004; Boehnke & Munoz, 2008). In birds, the OTv sends a similar signal to the primary visual area in the forebrain via the LGN and to the retina itself via the ION. This signal has high spatial resolution (small receptive fields) and could contribute to space-specific enhancement of forebrain processing of information in the context of spatial attention tasks (Wurtz et al., 2005).

The SCm in mammals sends a lower resolution (larger receptive fields), multimodal signal to other priority maps in the forebrain network: in the FEF and the LIP (Thompson & Bichot, 2005; Fecteau & Munoz, 2006; Bisley & Goldberg, 2010; Falkner *et al.*, 2010). The OTm in birds sends a similar signal not only to forebrain structures that respond to multimodal salience, but also to forebrain areas that analyze specific features of visual stimuli (Hellmann & Gunturkun, 2001; Luksch *et al.*, 2001; Nguyen *et al.*, 2004; Wylie *et al.*, 2009). The interaction of the SCm/OTm with areas in the forebrain network that evaluate and represent stimulus priorities may determine the next locus of attention.

The forebrain and midbrain networks normally cooperate in selecting the next locus of attention. The forebrain network typically controls the information that is processed in working memory, based on both stimulus-driven and endogenous information (Fig. 9, right, competitive selection). The essential contribution of the midbrain network is apparent under these conditions only when an animal is confronted with multiple, similarly salient stimuli. When this happens, the midbrain network is essential for signaling reliably the highest priority stimulus (McPeck & Keller, 2004; Lovejoy & Krauzlis, 2010).

In environments that contain distracting stimuli, activity that is driven by the distracters competes, moment-by-moment, with activity that is being enhanced by top-down signals for access to working memory (Fig. 9) (Munoz & Fecteau, 2002; Busch & VanRullen, 2010; Leber, 2010). In the event that a distracting stimulus (of any sensory modality) is highly salient due to its novelty, motion or intensity, the midbrain network has the capacity to override top-down influences by selecting and immediately initiating a shift of gaze toward the distracting stimulus. In a world in which the capacity to react rapidly to dangerous and unexpected stimuli makes the difference between life and death, this capacity provides a strong selective advantage to maintaining a highly effective midbrain network for controlling gaze and attention.

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Abbreviations

AGF	arcopallial gaze field
DLPFC	dorsolateral prefrontal cortex
FEF	frontal eye field
GABA	gamma amino butyric acid
Imc	nucleus isthmi pars magnocellularis
ION	isthmo-optic nucleus
Ipc	nucleus isthmi pars parvocellularis
LGN	lateral geniculate nucleus (also referred to as nucleus opticus in birds)
LIP	lateral intraparietal area
LTN	periparabigeminal lateral tegmental nucleus
OT	optic tectum
OTm	multimodal and motor optic tectum
OTv	visual optic tectum
PBN	parabigeminal nucleus
PULi	inferior pulvinar
PULd	dorsal pulvinar
RF	classical receptive field
ROT	nucleus rotundus
S_{in}	stimulus inside the receptive field
S_{out}	stimulus outside the receptive field
SC	superior colliculus
SCm	multimodal and motor superior colliculus
SCv	visual superior colliculus
SLu	nucleus semilunaris

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Figure 1.

The midbrain network for controlling spatial attention in mammals and birds. **Not shown are the substantia nigra pars reticulata and pars compacta.** Left: Layers of the mammalian SC and interconnections with the isthmic nuclei. Right: Layers of the avian OT and interconnections with the isthmic nuclei. Blue: visual component of the network: the superficial layers of the mammalian superior colliculus (SCv) and layers 1–10 of the avian optic tectum (OTv). Purple: multimodal and motor component of the network: the intermediate and deep layers of the superior colliculus (SCm) and layers 10–15 of the avian optic tectum (OTm); **the blue/purple hatching of layer 10 indicates that some neurons contribute to the OTv and others to the OTm.** Green: isthmic nuclei containing GABAergic neurons. Red: isthmic nuclei containing cholinergic neurons. Imc, nucleus isthmi pars magnocellularis; Ipc, nucleus isthmi pars parvocellularis; LTN, periparabigeminal lateral tegmental nucleus; PBN, parabigeminal nucleus; SLu, nucleus semilunaris. The nucleus isthmi disseminated (ID) is glutamatergic and receives input from the ipsilateral OT and projects to the contralateral OT.

Figure 2.

Focal inactivation of the monkey superior colliculus causes a location-specific deficit in sustained spatial attention. A) Monkeys were cued by a red circle to attend to the direction of a pulse of coherently moving dots and to report the direction of motion (red arrow) with an eye movement in the corresponding direction. They were trained to ignore both the orthogonally directed, coherent motion in the diagonally opposite quadrant (foil stimulus; yellow arrow) and the random motion in the neighboring quadrants. Blue: the region of the visual field affected by the inactivation. B) Eye saccade responses before SC inactivation. C) Eye saccade responses to the same stimulus configuration after SC inactivation. D) Comparison of responses before versus after SC inactivation when the cued stimulus was located within the inactivated portion of the visual field. E) Comparison of responses before versus after SC inactivation when the cued stimulus was located outside of the inactivated portion of the visual field. Modified from Lovejoy and Krauzlis, 2010.

Figure 3. Selected inputs and outputs of the SC/OT. A) Mammalian SC. B) Avian OT. Abbreviations: AGF, arcopallial gaze field; FEF, frontal eye field; ION, isthmo-optic nucleus; LGN, lateral geniculate nucleus; LIP, lateral intraparietal area; OTm, multimodal and motor layers of the OT; OTv, visual layers of the OT; PUL, pulvinar nucleus; ROT, nucleus rotundus; SCm, multimodal and motor layers of the SC; SCv, visual layers of the SC.

Figure 4. Schematic representation of circuits within the midbrain network in birds. Purple: projection from layer 10 in the OTm to the Ipc, SLu and Imc. Red: the projections of cholinergic neurons in the Ipc and SLu to both the OTv (blue) and OTm (purple). Green: the projections of GABAergic neurons in the Imc to the OTm (purple) and to the Ipc and SLu (red). Abbreviations: Imc, nucleus isthmi pars magnocellularis; Ipc, nucleus isthmi pars parvocellularis; OTm, multimodal and motor optic tectum; OTv, visual optic tectum; SLu, nucleus semilunaris. Based on data from Wang et al., 2004 and 2006.

Figure 5.

Global competitive surrounds in the barn owl OTm. A) Responses of a unit in the OTm to a looming dot (S_{in} : $8^\circ/s$) presented at different azimuthal locations, as shown on the left. B) Responses of the same unit to the S_{in} stimulus centered in the visual receptive field (RF) when presented simultaneously with a second, stronger looming dot (S_{out} competitor: $12^\circ/s$) located at different azimuths, as shown on the left. The S_{out} competitor, located anywhere in the visual field, strongly suppressed responses to the S_{in} stimulus. Modified from Mysore et al., 2010.

Figure 6.

Switch-like suppression of unit responses in the barn owl OTm by a distant, competing stimulus. A) Schematic of the experimental set-up viewed from above. The dashed circle indicates the unit's classical receptive field (RF). B) Top: raster plot of the unit's responses to a looming dot (S_{in} : 7°/s) centered in the RF. Bottom: raster plots of unit responses to S_{in} centered in the RF presented simultaneously with a second looming dot (S_{out}), of different speeds, located 30° to the side of the RF center. C) A competitor strength-response profile for the data shown in B. The black arrowhead indicates the strength of S_{in} . The response of the unit to S_{in} was suppressed powerfully and abruptly when the strength of the S_{out} stimulus exceeded the strength of the S_{in} stimulus. Modified from Mysore et al. (in press).

Figure 7.

Top-down signals from the forebrain gaze fields modulate sensory responses in the barn owl OTm. A) Experimental set-up. The AGF was microstimulated ($7 \mu\text{A}$; 25 ms; 200 Hz) while responses of an OTm unit to simultaneously presented auditory stimuli were recorded in the OTm. B) The effect of AGF microstimulation on auditory spatial tuning when the centers of the receptive fields (RF) in the AGF and OTm were aligned. Dashed lines: widths at half-max response without (black) and with (red) AGF microstimulation; black arrowhead: RF center for the OTm unit; red arrowhead: RF center for the AGF site; asterisks: $P < 0.02$ (paired t-test). C) Same as in B, but for an AGF microstimulation site that was not aligned with the RF of the OTm unit. Black arrowhead: RF center for the OTm unit; blue arrowhead: RF center for the AGF site. Modified from Winkowski and Knudsen, 2006.

Figure 8.

Functional properties of neurons in the barn owl Ipc. A) Switch-like suppression of unit responses by a distant, competing stimulus. The stimulus inside the receptive field (RF) was a looming dot ($4^\circ/\text{s}$ at 50% contrast). The stimulus outside the RF (S_{out}), presented simultaneously at a location 30° to the side of the RF center, was either a second 50% contrast looming dot of various speeds (red), a $4^\circ/\text{s}$ looming dot of various contrasts (blue), or a broadband noise burst of various sound levels (green). B) Periodic burst responses of an Ipc unit to a looming dot centered in the RF. Gray zone: duration of the visual stimulus; dashed lines: analysis window for response periodicity. C) Distribution of the peaks in the response power spectrum for 57 Ipc units. Dashed line: mean frequency of response periodicity = 36 Hz. Data from Asadollahi et al., 2010.

Figure 9.

A schema for the fundamental components of spatial attention. Representations (blue) encode sensory information about the world (green) as well as information about motor plans, internal state, stored memories, etc (not shown). All components of attention are carried out in the forebrain network (right). All components except working memory are also carried out in the midbrain network (left, red box). Information from working memory in the forebrain network is conveyed to the midbrain network by top-down signals, and retinotopic spatial information from forebrain representations is conveyed to the midbrain network. Salience and priority information in the midbrain network influences the forebrain representations, and competitive selection of a location in the midbrain network biases, and sometimes dominates, competitive selection for the next locus of attention in the forebrain network. Modified from Knudsen, in press.