On the importance of the transient visual response in the superior colliculus

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A salient event in the environment can initiate a complex orienting response that includes a shift in gaze. The midbrain superior colliculus (SC) contains the appropriate circuitry to generate and distribute a signal of the *priority* of this event, and co-ordinate the orienting response. The magnitude and timing of the short-latency transient visual response in the SC, when combined with cortical inputs signaling stimulus relevance and expectation, influences the type and latency of the orienting response. This signal in the SC is distributed to higher cortical areas to influence visual processing, to the reinforcement learning system to influence future actions, and to premotor circuits, including neck and shoulder muscles, to influence immediate action.

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Introduction

A friend waves to you from across the room. Your eyes respond to this visual motion by sending a signal directly, or indirectly via the cortex, to cells in the superior colliculus (SC) – a hub of sensory and motor processing in the middle of the brain. Some of these SC cells may already be at a heightened level of activity because you were scanning the crowd looking for her. The transient visual signal initiated by her wave arrives on these neurons to drive them over threshold to initiate a visual grasp reflex (*visueller Greifreflex* [1,2]) – a rapid shift of gaze

to align the high acuity retinal fovea with her face. Along with this overt orienting of gaze there are momentary changes in heart rate, blood pressure and brain wave activity, that are all part of a global orienting reflex that will prepare your body for possible action [3].

SC (optic tectum in non-mammals) circuitry and function is highly conserved phylogenetically [4–7], and the transient visual response in the SC is a rich, spatial signal, the properties of which determines the latency of orienting responses to visual targets [8–10]. Recent research has shown that this is owing to a unique convergence of inputs and processes that modulate this transient response, and by how this signal is broadcast to the rest of the brain through diverse connections with cortex, basal ganglia, and muscles that drive orienting responses. Here, we argue that this transient visual response in the SC has access to the appropriate inputs, intrinsic processing features, and outputs to generate and distribute a signal related to the behavioral priority of an event (after [11••]). By 'priority' we mean the convergence of bottom–up *salience* (i.e. stimulus related) information with the top–down *relevance* an event has for the observer based on expectations and prior experience.

The transient visual signal is generated by neurons with the appropriate input structure

Figure 1 highlights important brain areas involved in the orienting network that have been identified and reviewed in detail elsewhere [6,7,11••,12–15]. The SC is a critical hub in this circuit. It is a multi-layered structure (Figure 2a) that can be separated functionally into superficial, visual-only layers (SCs), and intermediate and deep layers (SCi) receiving convergent sensory, cognitive, and motor inputs. Visual inputs to the SCs arise from retina indirectly via the retino-geniculo-cortical pathway to primary visual cortex and early extrastriate areas, and directly from the retinotectal pathway. SCs neurons are organized into a retinotopically coded map of contralateral visual space and some SCs neurons project to the SCi directly [16]. Most neurons in the SC show an early (~40–70 ms latency), classic transient response (Figure 2a) to visual stimuli presented in a restricted region of the visual field (defining a response field). This response is also observed throughout the visual orienting network (Figure 1), including regions of visual, parietal and frontal cortex. Within the SCi, the transient visual signal merges with concurrent inputs from extrastriate cortex in addition to signals from auditory and somatosensory systems, and with information about context, arousal and motor plans
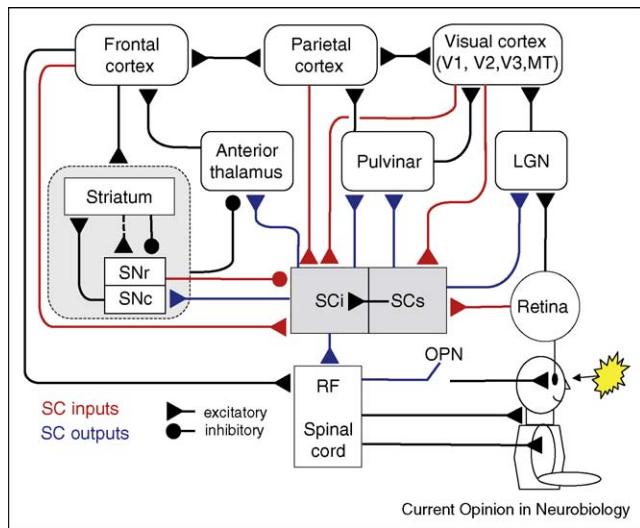
Circuitry for the orienting network with the superior colliculus (SC) situated as a hub. Red lines represent key SC inputs; blue lines represent key SC outputs. Abbreviations: LGN: lateral geniculate nucleus; OPN: omni-pause neuron gate; RF: reticular formation; SCi: SC intermediate layers; SCs: SC superficial layers; SNc: substantia nigra pars compacta; SNr: substantia nigra para reticulata.

from the basal ganglia and frontal and parietal cortices. This extensive convergence has even led some to conclude that the SC is the only logical substrate for conscious self-awareness [17].

Neurons distributed throughout the SCi increase their discharge before and during saccades, and are organized into a retinotopically coded visuomotor map [18] specifying saccade vectors into the contralateral visual field. A subset of these, visuomotor neurons, discharge a transient visual response to a stimulus in their response field, and a separate burst of action potentials time-locked to initiation of a saccade to that location (Figure 2a). There is a close spatial correspondence between the visual and motor response fields of these neurons [18], which serves to coordinate action by placing a spatially coded visual response directly onto neurons that project [19] to the premotor circuitry in the brainstem reticular formation and upper cervical spinal cord. Thus, visual inputs signaling salience can combine with goal-oriented signals emanating from frontal and parietal cortex, and the basal ganglia, to influence behavioral responses. It is these visuomotor neurons within SCi that appear to carry the transient visual response related to priority [11••,20•].

The transient visual signal represents the when and where, but not the what

A priority signal cannot be exhaustive in what it represents. Ideally, it should mark the time, place, and

priority of the event as a tag to be sent to other brain areas focused on processing stimulus features [11••]. The transient visual signal in the SC is constrained to an orderly spatial map (Figure 3a), and is of short-latency owing to its direct input from the earliest stages of visual processing. It is dependent on factors influencing the physical distinctiveness (salience) of the stimulus such as contrast, with the transient visual response to brighter stimuli being greater in magnitude and occurring earlier in time [10,21]. The signal is not particularly selective, however, for visual features such as color, orientation, shape, motion velocity or duration [7,22]. The early part of the signal is also blind to whether a stimulus in its receptive field is a target or distractor stimulus, if each is equally likely. It is only 20–30 ms later, after further cortical processing, that such stimuli can be discriminated by SCi neurons [23,24]. This pattern of sensitivity is consistent with the transient visual response acting as a timestamp of a prioritized event at a specific location.

The transient visual signal can cause fast action directly

Under evolutionary pressure, a priority signal would be required to stimulate immediate action, either towards stimuli of interest (e.g. prey) or away from perilous stimuli (e.g. large looming things). The SC mediates these two fast responses through access to different motor output channels [4,5]. Unlike other parts of the visual orienting network (see Figure 1), the visuomotor output neurons of the SCi have direct projections to the premotor circuitry in the brainstem and spinal cord to influence action directly [19,25]. The level of excitability within SCi at the moment that the incoming transient visual response arrives plus the magnitude of this response itself will ultimately determine the behavioral response elicited, because the magnitude of the response is correlated with the latency of saccade initiation [8,9]. It is believed that a saccade is initiated when activity among saccade-related neurons in the SCi and FEF, caused by both pre- and post-target processing, accumulates toward some threshold level of activity at the map location specifying that saccade vector [26].

When an observer anticipates the location and time of target appearance, the pre-target level of activity of saccade neurons in the SCi is elevated [27,28], and the transient response can exceed the threshold to initiate an *express-saccade* (dashed line in Figure 2b), which in primates occurs with a latency approaching the minimal sensory-motor conduction times (70–100 ms) [8,29,30]. In this case the visual transient itself is transformed into the motor burst. If pre-target activity is low, the transient visual response will not exceed saccade threshold and the system will only trigger a regular latency saccade (solid line in Figure 2b). Thus, distributions of saccadic reaction times can be bimodal (e.g. Figure 2c), with the peak magnitude of the visual

Figure 2
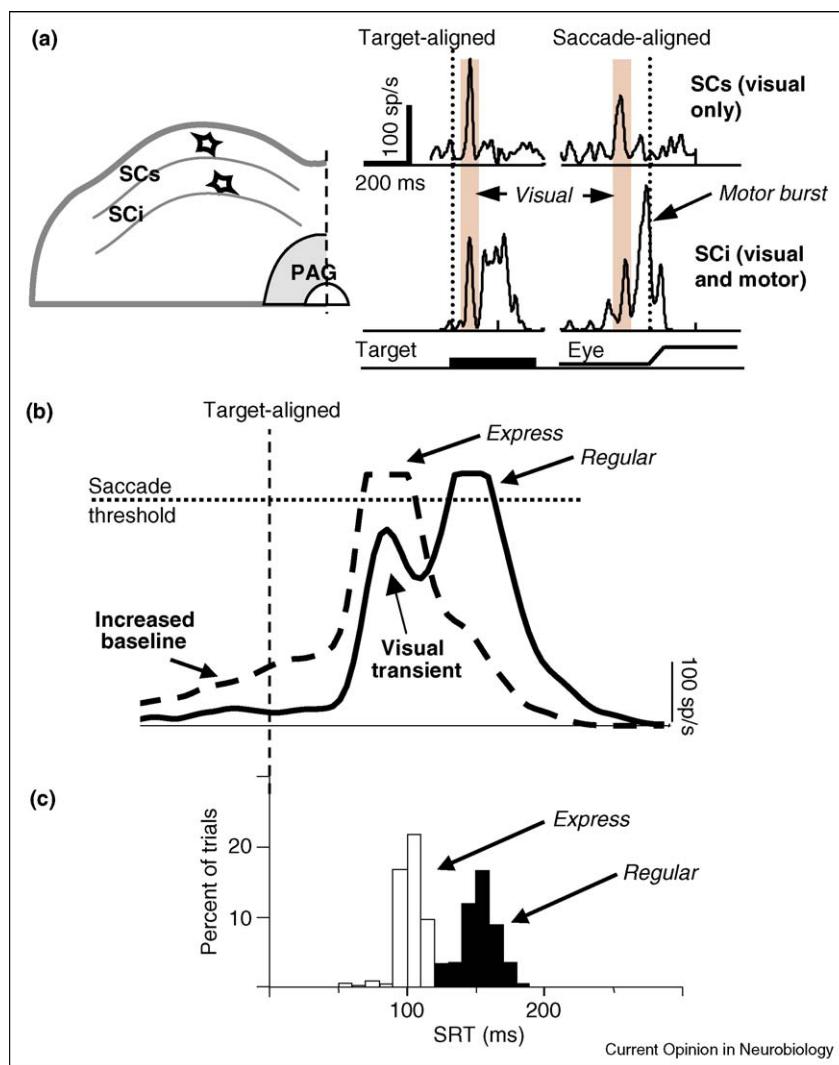
(a) Schematic of the functional sublayers within the SC: superficial (SCs) and intermediate (SCi). The responses of representative neurons in each layer during a saccade to a visual target, aligned on either target appearance or saccade onset. The red transparent bar highlights the transient visual response of these neurons. (b) Saccades are initiated only when the activity of saccade neurons in the SCi exceeds a threshold. Express saccades are triggered when the visual transient itself exceeds saccadic threshold (dashed trace), regular latency saccades require the addition of voluntary drive (the motor burst) to push the activity over threshold (solid traces). (c) This results in a bimodal distribution of saccadic reaction times.

response correlated to the type and timing of the orienting response generated [8,9]. Removal of the SC abolishes the ability to generate express saccades [31], but not longer-latency saccades. When the individual does not want to orient to a visual stimulus, then suppressing baseline activity, even momentarily, can prevent the transient visual response from achieving threshold [13], and once this transient signal clears the system, the threat to orient is removed. Either way, it is the resultant magnitude of the transient visual response that dictates the immediate actions that will occur.

The transient visual signal is modulated by cortical and basal ganglia inputs

A priority signal ought to have inputs which can increase or decrease its magnitude when priority changes. The incoming transient visual signal builds upon baseline activity in SCi neurons that can be very high if there is strong expectation, motor preparation, and/or reward signals [32] that emerge via reduced inhibition from substantia nigra par reticulata (SNr) in the basal ganglia, and/ or through enhanced excitatory inputs from frontal or parietal cortex. The baseline can be very low if there is strong suppression coming from the basal ganglia via the

Figure 3
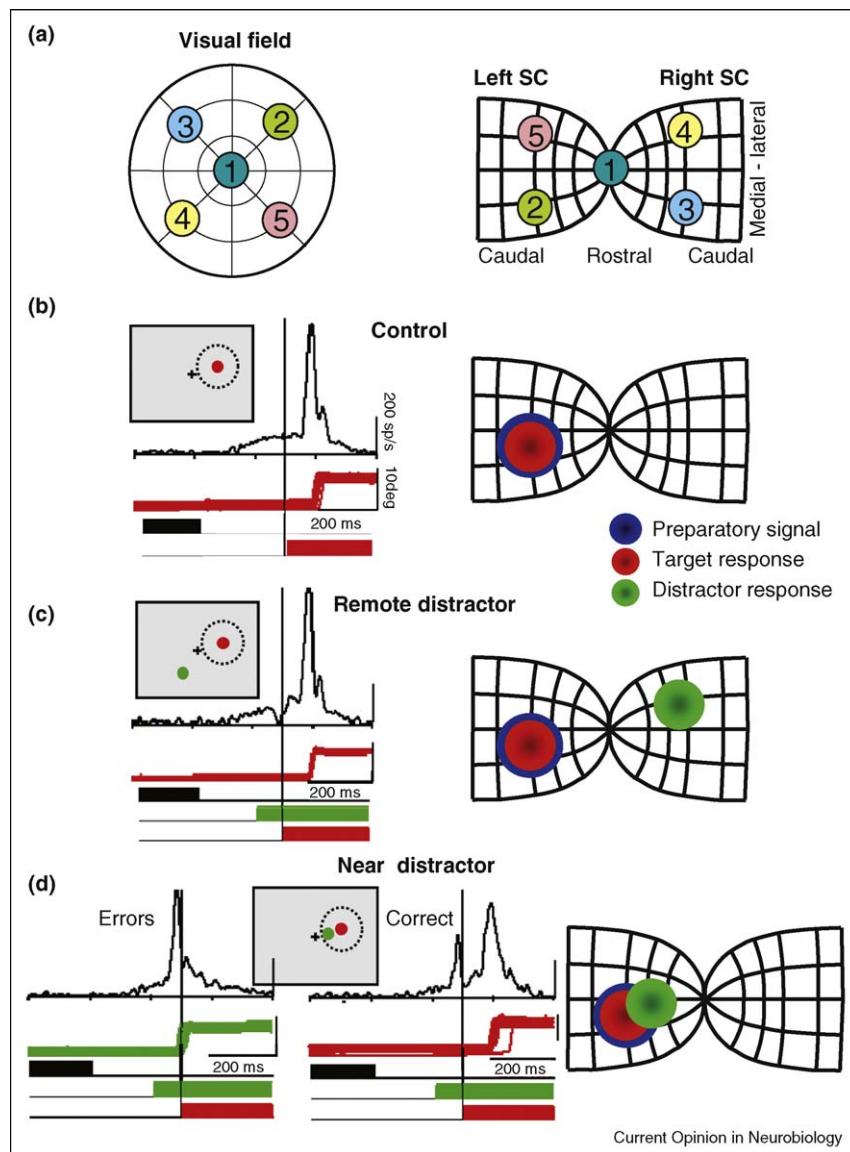
(a) Schematic correspondence of locations in visual space with locations on the SC retinotopic map. **(b–d)** Effects of combining bottom–up visual transient signals (red and green) with top–down motor preparation signals (blue). Left side illustrates neural responses of a visuomotor neuron with eye position traces and stimulus sequence below. The schematic on the right side highlights active regions on the SC map for different target (red) and distractor (green) conditions. **(b)** Perfect temporal and spatial predictability of a target with no distractor presented. The transient visual response (red circle) overlaps with the region of preparation (blue circle) and express saccades are triggered. **(c)** Presentation of a remote distractor (green circle) 100 ms prior to target appearance has little effect on the transient visual response and the generation of express saccades. **(d)** When the distractor is presented near to the target, the visual response to the distractor often combines with the spatially tuned motor preparation signal to trigger reflexive express-saccade errors to the distractor (green traces). If the visual response to the distractor does not exceed threshold it can be ignored and correct saccades are made to the target (red traces). **(b–d)** Adapted with permission [34•].

SNr [13,33]. A recent experiment has demonstrated that motor preparation effects owing to target expectation are spatially tuned and interact directly, possibly via lateral inhibitory connections within the SC, with transient visual inputs to dictate orienting responses [34•]. Monkeys were trained to make saccades to a target that was very predictable, both spatially and temporally. Such conditions elicit high rates of express saccades [28,29] (Figure 3b). On some trials, a green distractor was presented 100 ms earlier, but at various unpredictable locations from the expected red target. The proportion of express saccades made to this distractor was graded with its distance away from the future target location; the highest number of distractor-directed errors were made to

near-target distractors (Figure 3d), and no distractor-directed errors were made to remote-target distractors (Figure 3c). The peak of the transient visual response to the distractor determined when an error would be made. This result is important for two reasons – it shows that the top–down signals within the SCi are spatially tuned and these signals can combine with the sensory responses directly to trigger orienting.

The transient visual signal is influenced by other senses

The transient response would not be of much use as a global signal of event priority if it only responded to visual stimuli. Within the SCi there are well known auditory and somatosensory inputs whose reference frames are transformed to be in register with the retinotopic representation [7]. When these auditory and tactile signals are spatiotemporally congruent, they can also merge with the visual transient to raise its magnitude and shorten saccade latencies [35].

## The transient visual signal reduces with repetition

Stimuli that are repetitive will decrease in novelty, causing the repeating stimulus to lose priority. The simplest way the brain has to track this is via sensory adaptation [36] or habituation [37], whereby stimulus repetition without consequence reduces response magnitude. Visual responses in both the SCs and SCi [38] diminish with even a single stimulus repetition, and the reduction in the signal is sufficient to delay saccadic reaction time [9,11••,39,40]. This phenomenon also occurs in cortex, because visual responses in area V4 [41] and frontal eye field [42], particularly the transient component, also diminish with repetition. This type of decrement is not overcome by the stimulus being the target of a saccade [42]. Possibly owing to another mechanism, visuomotor neurons in the SCi may habituate so strongly that they stop responding altogether to a repeating irrelevant stimulus [43]. This can occur in anaesthetized animals whose cortex has been removed, suggesting that a component of this mechanism may be intrinsic to the SC [44]. The neuron may recover this response with time, or by signals which 'dishabituate' it [37], such as when the stimulus location becomes the target of a saccade (e.g. 'enhancement effect' [21,45]), when stimulus properties change sufficiently (e.g. increased luminance, change in motion direction [43]), or when another sensory stimulus is presented elsewhere [46].

The transient visual signal has the correct output structure to distribute a priority signal

For a priority signal to be useful it must have direct access to other brain regions that require that information. Through its extensive connections to extrastriate, parietal and frontal cortex via the pulvinar [47,48] and anterior thalamus [49], and via direct connections to the basal ganglia, and brainstem circuitry controlling action, the SC is poised to distribute its spatially constrained priority signal to almost all systems (Figure 1). Even when no action is taken towards a salient peripheral stimulus, that stimulus is still 'noticed' and oriented towards covertly (see [11••], for review), which has consequences on future

Figure 4
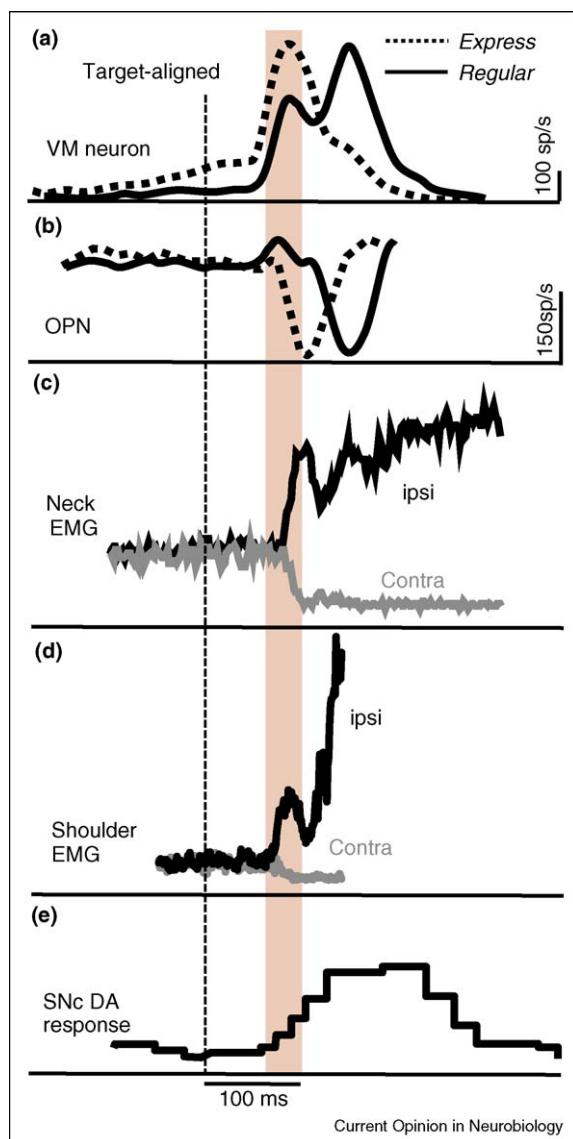
Comparison of short-latency transient visual responses in various SC output structures. **(a)** Visuomotor output neuron in the SCi has separate visual and motor bursts for regular saccades and a single burst at visual conduction latency for express saccades. **(b)** Responses for express and regular latency saccades for an omni-pause neuron (OPN) in the brainstem reticular formation. Short-latency visual responses on the OPNs are associated with regular latency saccades, but not express saccades [50]. **(c)** Short-latency transient visual responses recorded from a small dorsal neck muscle OCI [51••]. **(d)** Short-latency transient visual responses recorded from a shoulder muscle posterior deltoid. **(e)** The short-latency transient response of dopaminergic cells of the SNc (adapted with permission [56••]).

actions. This is because the transient visual response in the SC still propagates throughout the orienting system whether it is selected for action or not. Figure 4 illustrates the transient visual responses of an SCi visuomotor neuron (Figure 4a) and similar responses in some structures to which it projects (directly or indirectly). Note that all responses are short-latency (<100 ms). The SCi projects to the brainstem and spinal cord premotor circuitry for controlling eyes, head, and limb or body movements [14,19,25]. The eye movement system is controlled by a gate in the brainstem reticular formation created by the omni-pause neurons (OPNs; Figure 4b), which discharge strongly during fixation in order to inhibit the premotor burst neurons and prevent saccades. When threshold activity level is surpassed in the SCi, these OPN neurons are inhibited briefly, allowing the saccadic burst command to be relayed to the extraocular muscle motorneurons to generate the saccade. Interestingly, even some OPNs inherit the transient visual response (see Figure 4b, solid line) [50], although it is only visible when regular latency saccades occur (the OPNs are inhibited at that time during express saccades, Figure 4b, dashed line).

Recently it was discovered that the circuitry controlling the neck musculature has no such gate so that visual responses from the SCi can travel through the premotor circuit to the muscles even when no orienting response is triggered [51**,52*]. A lateralized transient visual response with a fixed latency less than 100 ms after target appearance can be recorded from dorsal neck muscles around the C1–C2 cervical joint that rotate the head (Figure 4c). This response can serve to 'warm up' head musculature over a short time span immediately following target appearance while a decision to move is formed. Like the visual response in the SCi, the magnitude of the visual response on neck muscles is correlated with the reaction time of the gaze shift [51**], and its magnitude is similarly modulated by previous events thought to be related to covert orienting effects [52*]. When a saccade to the stimulus is suppressed, this visual response on neck muscles can even initiate micro head movements (gaze remains steady owing to the vestibular-ocular reflex) [52*]. Even more intriguing, a transient visual response has now been identified on shoulder musculature (Figure 4d). This response occurs at short-latency, is lateralized, and its magnitude correlates with reaching movements to the visual targets [53,54].

The transient visual signal is projected to the reinforcement learning circuitry in the basal ganglia

It is important for a priority signal to provide input to the reinforcement learning circuitry so that the organism can learn about the novel stimuli generated by their actions. If those actions are rewarded, they will be repeated and the resultant stimulus may change in priority. Recently it has been shown that the visual transient in the SCi is pro-

jected monosynaptically [55] to the dopaminergic neurons of the substantia nigra pars compacta in the basal ganglia (Figure 1). The transient visual response of the SCi provides the main afferent source for the 'short-latency dopamine response' (Figure 4e) that marks the onset of novel or prioritized stimuli for use by the reinforcement learning system [56**] (see [57**] for review), and it has properties ideally suited to do so. As we have described above, the transient visual response in the SCi is sensitive to bottom up saliency, is enhanced by expectation and motor preparation, and adapts or habituates with stimulus repetition – its magnitude can be thought to represent the priority of a stimulus even prior to inspection via foveation. Thus, the dopaminergic system will get activated strongly by stimuli deserving of future consideration of action, and weakly by those that do not.

Conclusions
We have proposed that the transient visual response in the SC contains the appropriate input structure, intrinsic processing features, and distribution network to be the source of a priority signal [11**] that marks the onset of important events. This transient signal may also represent the substrate of covert orienting – the obligatory 'noticing' of a stimulus in the periphery without actually shifting gaze towards it. Important processing related to signal priority is observed in many places, such as frontal and parietal cortex, which influence the transient visual response in the SC. However, it is the resultant SC signal (the amalgam of all these inputs) that has the ability to influence behavior directly via its control of gaze shifts, or indirectly by sending the visual response to warm up muscles for possible action, and to stimulate neurons involved in reinforcement learning to contribute to future action [57**].

Another argument in favor the SC carrying this signal is evolutionary. The function of sorting out stimulus priority was already present in the SC of species with far less visual cortex [5] and it seems unlikely that visual cortex would have evolved and expanded in mammals as a parallel independent system. It makes more sense that visual cortex evolved to exploit the already present signals in the SC, a proposition supported by the evidence presented here.

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57. Redgrave P, Gurney K: **The short-latency dopamine signal: a**
•• **role in discovering novel actions?** *Nat Rev Neurosci* 2006, **7**:967-975.
This thought-provoking review described results (e.g. [55,56••]) demonstrating that the SCi is the afferent source of short-latency dopamine (DA) response. This signal is too early to represent a reward prediction error signal – the dominant view in the reinforcement learning field – but may instead be used to identify actions or contexts which cause unpredicted sensory stimuli, facilitating the learning of novel actions.