BEHAVIORAL NEUROSCIENCE

Activity in the superior colliculus reflects dynamic interactions between voluntary and involuntary influences on orienting behaviour

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Abstract

Performance in a behavioural task can be influenced by both bottom-up and top-down processes such as stimulus modality and prior probability. Here, we exploited differences in behavioural strategy to explore the role of the intermediate and deep layers of the superior colliculus (dSC) in covert orienting. Two monkeys were trained on a predictive cued-saccade task in which the cue predicted the target's upcoming location with 80% validity. When the delay between cue and target onset was 250 ms, both monkeys showed faster responses to the uncued (Invalid) location. This was associated with a reduced target-aligned response in the dSC on Valid trials for both monkeys and is consistent with a bottom-up (i.e. involuntary) bias. When the delay was increased to 650 ms, one monkey continued to show faster responses to the Invalid location whereas the other monkey showed faster responses to the Valid location, consistent with a top-down (i.e. voluntary) bias. This latter behaviour was correlated with an increase in activity in dSC neurons preceding target onset that was absent in the other monkey. Thus, using the information provided by the cue shifted the emphasis towards top-down processing, while ignoring this information allowed bottom-up processing to continue to dominate. Regardless of the selected strategy, however, neurons in the dSC consistently reflected the current bias between the two processes, emphasizing its role in both the bottom-up and top-down control of orienting behaviour.

Introduction

When faced with a particular task, we rely on a variety of factors including prior experience and expected outcome to develop the appropriate strategy necessary to accomplish this task. Individuals often weigh these factors differently and so it should come as no surprise that identical conditions can yield different results from one subject to the next. By examining the different strategies and their associated outcomes, we may gain valuable new insights into the neural mechanisms underlying this behaviour.

The current study takes advantage of different behavioural outcomes observed in two monkeys trained on a predictive cued-saccade task (Posner, 1980) in order to further explore the neural mechanisms involved in covert orienting. Our task featured a cue that indicated the probable location of an upcoming saccadic target with 80% validity (Fig. 1A). The monkey's behaviour in this task can be influenced by both bottom-up (i.e. involuntary) and top-down (i.e.

voluntary) components: a bottom-up mechanism delays the subject's ability to generate an eye movement to the target should it appear at the same location as the cue (i.e. inhibition of return, IOR; see Klein, 2000; Fecteau & Munoz, 2006 for review). However, because the cue provides information about where the target will probably appear, there is an opportunity for top-down mechanisms to override this involuntary process and facilitate a response to the cued location (i.e. attentional facilitation; see Wright & Ward, 1998; Wright & Richard, 2000; Fecteau & Munoz, 2006 for review).

We manipulated the delay between cue and target appearance in order to influence the relative contributions of these two mechanisms. The respective 'strategy' is operationally defined as the 'sum' of the bottom-up and top-down mechanisms, assessed using the behavioural outcome. If the monkey is faster to orient to the cued (Valid) location, the contribution of top-down processing probably exceeds that of bottom-up processing. If the animal is faster to the uncued location (Invalid), bottom-up processing is probably dominating. While the monkeys performed this task, we recorded activity from visually-responsive neurons in the intermediate and deep layers of the superior colliculus (dSC), a structure involved in coordinating orienting behaviour (see Sparks, 1999; Munoz *et al.*, 2000 for review) that is also believed to play a role in covert attention (Kustov & Robinson,

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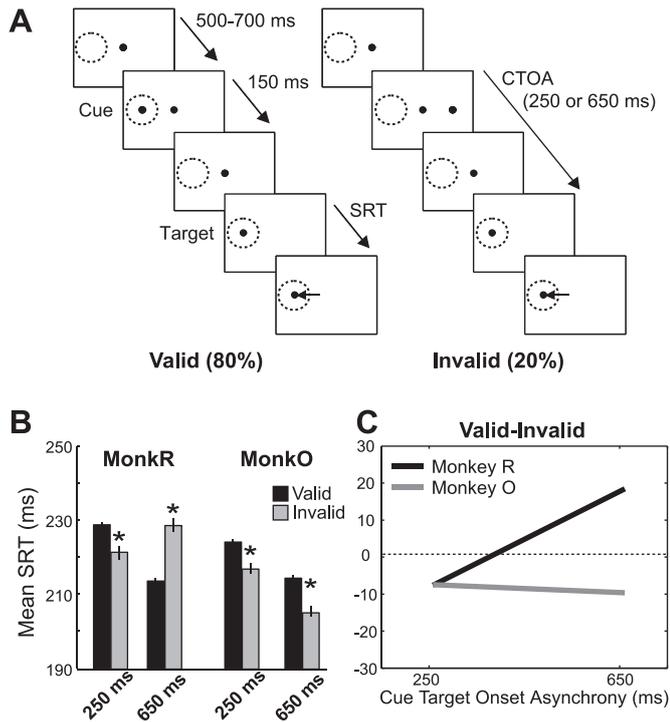
FIG. 1. (A) Schematic representation of the predictive cue–target saccade task used in this study. Monkeys were required to maintain central fixation while a visual, auditory or audiovisual cue was presented to the response field of the neuron (indicated by dashed circle) or to the opposite side. A visual or audiovisual target was presented after a short CTOA (250 or 650 ms, in separate blocks) to which the monkeys were required to generate a saccade. The target could appear at either the same location (Valid condition; 80% of trials) or to the opposite side (Invalid condition; 20% of trials). (B) Mean (± SEM) SRTs in the task. The two monkeys completed a total of 18 501 correct trials over the course of the recording sessions (monkey R, 6935; monkey O, 11 566). Black bars indicate trials in which the cue and target appeared at the same location (Valid condition); grey bars indicate trials in which the cue and target appeared at opposite locations (Invalid condition). *$P < 0.05$ for difference between the two conditions (Wilcoxon rank-sum test). (C) Difference in mean SRT between Invalid and Valid conditions for both monkeys. Values < 0 indicate shorter SRTs in the Invalid condition (i.e. IOR). Values > 0 indicate shorter SRTs in the Valid condition (i.e. attentional facilitation).

1996; Ignashchenkova et al., 2004; Fecteau et al., 2005; Muller et al., 2005). Here, we show that the neural correlates of both top-down and bottom-up control of behaviour are evident in the dSC.

Materials and methods

All procedures were approved by the Queen's University Animal Care Committee and were in accordance with the Canadian Council on Animal Care policy on the use of laboratory animals. Two adult male rhesus monkeys (Macaca mulatta, 9–12 kg) were prepared for chronic experiments in a single aseptic surgical session under isoflurane (1–2%) anaesthesia (see Bell et al., 2005 for details). Briefly, scleral search coils, used to monitor eye position (Robinson, 1963; Judge et al., 1980), were implanted. A craniotomy was performed and a stainless steel chamber centred on the midline and tilted 38–40° posterior of vertical to allow access to both superior colliculi (SC) was mounted within an explant of dental acrylic secured to the skull with stainless steel screws. A stainless steel holder, used to stabilize the head during recording sessions, was also embedded in the explant.

Monkeys were given a course of antibiotic and analgesic treatment and monitored closely following surgery. They were given at least 2 weeks to recover before they began behavioural training.

Monkeys were trained to perform a predictive cued-saccade task (Fig. 1A). Cue stimuli consisted of visual (0.05 cd/m²) and/or auditory (43.5 dB, A-weighted) stimuli (presented in spatial alignment on combined trials), presented either to the response field of the neuron being examined (see below) or to the diametrically opposite location. Target stimuli were either visual or audiovisual. Performance in this task was most strongly influenced by cue condition (Valid vs. Invalid). Consistent with our previous findings (Bell et al., 2004), auditory cues elicited no significant changes in behaviour or neural activity across cue condition. Further, there were no significant differences between visual and audiovisual cue or target trials in this task. Therefore, we have omitted the auditory cue trials and grouped across cue and target modality. In 80% of the trials, the cue and target appeared in the same location (Valid condition; left panel, Fig. 1A) and in 20% of the trials, the cue and target appeared in opposite locations (Invalid condition; right panel, Fig. 1A). The delay between cue and target onset (cue–target onset asynchrony, CTOA) was either 250 or 650 ms.

Recording techniques and response field mapping

Single-neuron activity was recorded extracellularly in both SC with tungsten microelectrodes (Frederick Haer, Bowdoin, ME, USA) with impedances of 0.5–3 MΩ at 1 kHz. Electrodes were driven by a hydraulic microdrive (Narishige Inc, East Meadow, NY, USA) through stainless steel guide tubes supported by a Delrin grid placed inside the recording chamber (Crist et al., 1988). Single-neuron activity was sampled at 1 kHz after passing through a window discriminator (Bak Electronics, Mount Airy, MD, USA), which excluded action potentials that did not meet both amplitude and temporal constraints. Control of the behavioural paradigms as well as storage of eye position and neural activity was achieved by a Pentium PC running a real-time data acquisition software package (REX Ver 5.4; Hays et al., 1982). Eye position was sampled at 500 Hz.

To approximate a neuron's visual response field, a hand-held ophthalmoscope was used to back-project moving spots and bars of light onto the tangent screen while the monkey maintained central fixation. In many instances, visual stimuli were also systematically presented throughout the visual field. The centre of the response field was defined as the point at which the maximum visual response was elicited.

Criteria used to determine neuron classification and laminar distribution are described elsewhere (Bell et al., 2004, 2005). Briefly, neurons in the intermediate layers of the SC were classified as sensory only, sensory–motor or motor only based on their sensory and motor response properties, assessed using the cue- and saccade-aligned responses at the 650-ms CTOA. A given neuron was classified as visually and/or aurally responsive when the magnitude of its cue-aligned activity (peak response 0–150 ms following cue onset) was significantly greater than baseline (defined as mean activity 100–0 ms prior to cue onset; Wilcoxon rank-sum test, $P < 0.05$). A neuron was defined as saccade-related when the peak saccade-aligned activity (± 10 ms surrounding saccade onset) consistently exceeded 80 spikes/s for saccades to the neuron's preferred direction. The experimenter later verified all classifications to ensure accuracy and consistency.

Laminar distribution of the neurons was estimated based on activity landmarks and relative depths. Neurons deeper than 1500 μm below the dorsal-most superficial border of the SC or that displayed auditory and/or motor activity were classified as intermediate-layer neurons.

Data analysis

All data analysis was carried out on a Sun Ultra 60 Sparcstation using user-generated programs and a Pentium PC running MATLAB software (Mathworks Inc., Natick, MA, USA). Saccade onset and offset were identified on the basis of velocity and acceleration criteria. Neuronal responses were analysed using spike density functions that were constructed by convolving each recorded action potential with the following function, based on an exponential growth–decay function:

$$A(t) = \left[1 - \exp\left(\frac{-t}{\tau_g}\right)\right] \times \left[\exp\left(\frac{-t}{\tau_d}\right)\right] \quad (1)$$

where the activation level A varies as a function of time t, according to τ_g, the growth time constant that was set to 1 ms, and τ_d, the decay time constant that was set to 20 ms. The individual pulses were summed to generate a single spike density function for each trial.

For population analyses of the behavioural and neuronal data, repeated-measures ANOVAs were used, including the following factors: CTOA (250 vs. 650 ms) and cue condition (Valid vs. Invalid). Simple effects were analysed with pair-wise Wilcoxon signed rank-sum tests. In all instances, an alpha of < 0.05 was chosen as significant, with results of < 0.10 discussed when of theoretical interest. For display purposes only, spike density functions are shown as floating averages of 10-ms bin widths.

Results

At the 250-ms CTOA, despite the predictive nature of the cue, both monkeys generated saccades with shorter saccadic reaction times (SRTs) when the target was presented to the uncued location (Invalid condition) compared to the cued (Valid) location (Fig. 1B). Subtracting the mean SRT for the Valid condition from that for the Invalid condition revealed a significant opposite-side advantage, characteristic of IOR, in both monkeys (Fig. 1C). When the CTOA was increased to 650 ms, monkeys R and O produced two very different patterns of behaviour. Monkey R generated saccades with significantly shorter SRTs in the Valid condition, while monkey O continued to generate saccades with shorter SRTs in the Invalid condition (all $P < 0.05$). Further, monkey O showed a significant effect of CTOA across all trial types (ANOVA: $F_{1,2} = 16.072$, $P < 0.005$) such that all saccades, regardless of cue condition and stimulus modality, were generated with significantly shorter SRTs at the 650-ms CTOA than at the 250-ms CTOA.

The two behavioural trends observed in this study were well represented in the activity of neurons recorded from the dSC ($n = 28$). The strong opposite-side advantage observed in both monkeys at the 250-ms CTOA was associated with a marked reduction in the magnitude of the target-aligned response for Valid trials compared to Invalid trials (Fig. 2A and B). By contrast, the same-side advantage observed in monkey R at the 650-ms CTOA was associated with a steady rise in activity following the cue-aligned response that peaked immediately prior to the onset of the target-aligned response (see arrow in Fig. 2C). This increase in 'pretarget' activity was not observed in monkey O (Fig. 2D). Interestingly, the reduction in average SRT observed in monkey O at the 650-ms CTOA was associated with a pronounced increase in average target-aligned activity (not shown; $P < 0.0001$).

To quantify the changes in neural activity across the population, we measured the peak spike density 50–150 ms following target onset for both CTOAs ('Target Epoch'; dark bars, Fig. 2) and the peak activity
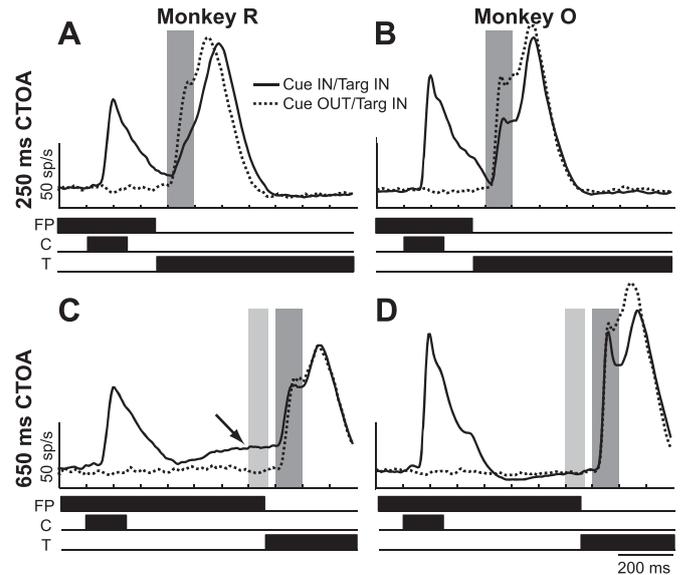

FIG. 2. (A–D) Population activity for neurons recorded from the dSC for monkeys R and O. Each panel shows data from trials in which the cue and target appeared in the given neuron's response field (Valid condition, solid traces) and trials in which the target but not the cue appeared in the response field (Invalid condition, dotted traces). Dark bars indicate the target epoch, light bars indicate the pretarget epoch. All traces are aligned on cue onset. FP, fixation point; C, cue; T, target.

from −50 to +20 ms surrounding target onset for the 650-ms CTOA ('Pretarget Epoch'; light bars, Fig. 2). Figure 3A–C plots the differences in mean peak firing rates for the different epochs in the Valid and Invalid conditions. Pretarget analysis was not performed on data obtained at the 250-ms CTOA to avoid confounding activity with the cue-aligned response. At the 250-ms CTOA, both monkeys showed significantly greater target-aligned activity in the Invalid condition than the Valid condition (Fig. 3A, $P < 0.05$). The differences in magnitude of the target-aligned response between the Valid and Invalid conditions were no longer significant at the 650-ms CTOA for monkey R but remained significant for monkey O (Fig. 3B, $P < 0.05$). Similarly, the effect of cue condition on pretarget activity was quite different between the two monkeys. For monkey R, significantly greater pretarget activity was evoked when the cue was presented into the response field of the neuron compared with when it was presented to the opposite side (Fig. 3C). Monkey O did not show any significant increase in pretarget activity with respect to cue location.

To determine the relationship between neural activity and behaviour, we first calculated trial-by-trial Pearson correlation coefficients between the target-aligned response at the 250-ms CTOA and SRT for each neuron (Fig. 3D). Ninety-six per cent of neurons (24/28) showed negative correlation values (mean r value, −0.24) of which 50% (14/28) were statistically significant, indicating that the target-aligned response was strongly correlated with SRT. The identical relationship was observed at the 650-ms CTOA (Fig. 3E). Pretarget activity did not correlate directly with SRT (Fig. 3F). However, a strong positive correlation with the magnitude of the target-aligned response was observed (Fig. 3G). Ninety-six per cent of neurons (27/28) had positive correlation coefficients (mean r value, +0.27) of which 57% (16/28) were statistically significant ($P < 0.05$). Importantly, while the two monkeys exhibited different behaviour at the 650-ms CTOA, data collected from both monkeys revealed the identical pattern of
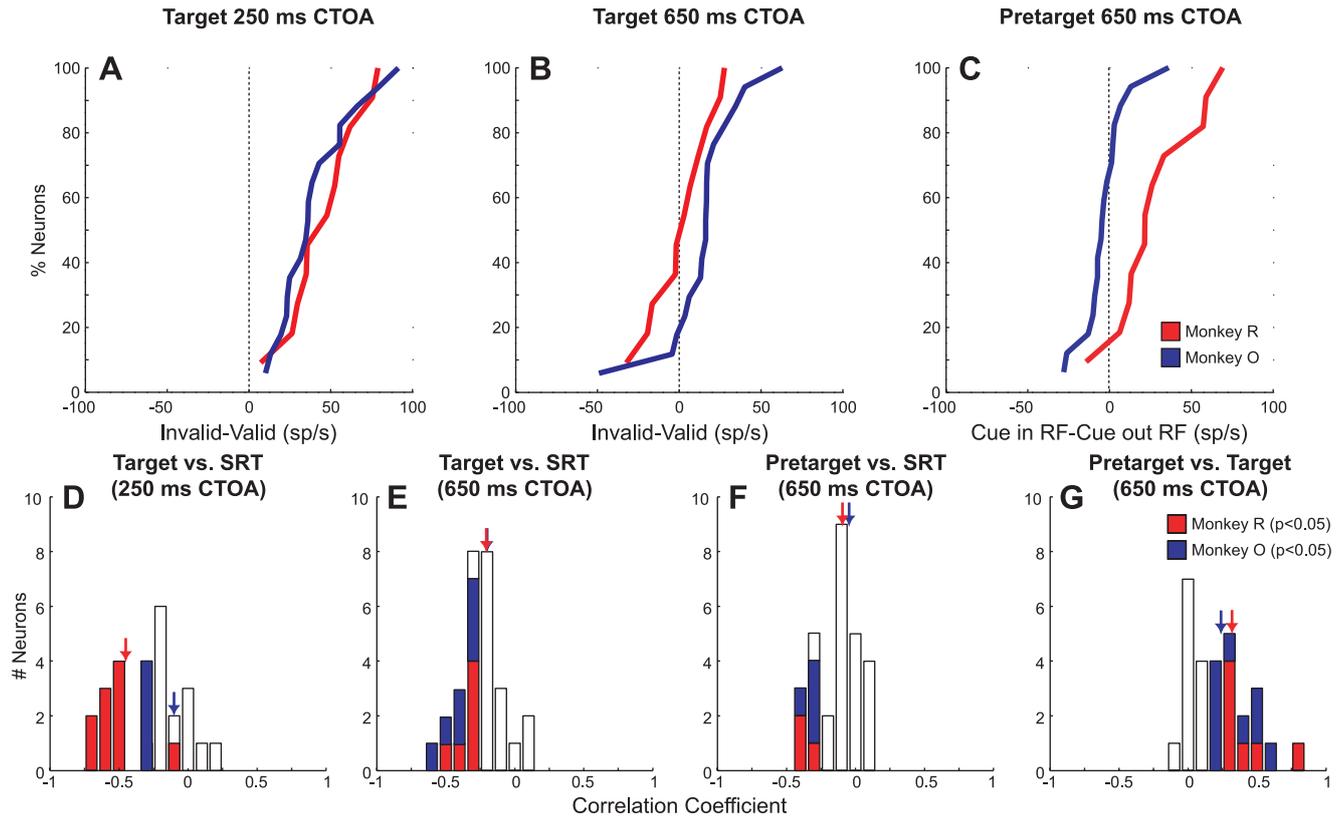
FIG. 3. Analysis of neural activity in the predictive cued-saccade task. (A) Invalid advantage at the 250-ms CTOA correlated with reduced target-aligned response in the dSC. Data are plotted as the cumulative probability of the differences between the mean response elicited in the Valid condition subtracted from that in the Invalid condition on a neuron-by-neuron basis. The majority of neurons showed stronger responses in the Invalid condition, as indicated by the significant rightward shift of the traces (Wilcoxon signed-rank test; $P < 0.05$). (B) No significant difference in the target-aligned response for monkey R at the 650-ms CTOA (Wilcoxon signed-rank test, $P > 0.05$). (C) Valid advantage observed in monkey R at the 650-ms CTOA correlates with increased pretarget activity in the dSC (red trace; Wilcoxon signed-rank test, $P < 0.05$). No such shift was observed in neurons recorded from monkey O (blue trace; $P > 0.05$). (D and E) SRT was strongly correlated with the magnitude of the target-aligned response at both the 250- and 650-ms CTOA. Histogram of Pearson correlation coefficients for the population of neurons analysed, correlating SRT with the magnitude of the target-aligned response. Negative values indicate that shorter SRTs were correlated with greater target-aligned responses. Pretarget activity was not correlated with (F) SRT but was positively correlated with (G) the magnitude of the target-aligned response. Individual neurons with significant correlation coefficients are shown as solid red bars for monkey R and solid blue bars for monkey O ($P < 0.05$). Vertical arrows indicate the mean correlation coefficient for monkey R (red) and monkey O (blue).

correlations between neural activity and SRT (as opposed to one monkey driving the effects).

In summary, the opposite-side advantage observed at the 250-ms CTOA was associated with a reduction in the magnitude of the target-aligned response in both monkeys (Figs 2 and 3). At the 650-ms CTOA, monkey R showed an increase in pretarget activity that was associated with a same-side advantage in behaviour (Fig. 1B). Monkey O did not show any increase in pretarget activity, nor did this monkey show the same-side advantage in behaviour at this CTOA.

Discussion

The traditional approach to monkey neurophysiological experiments is to train the animals to the point where their behaviour reaches a certain performance criterion as determined by the experimenter, at which point data collection begins. However, with more sophisticated tasks, individual monkeys may adopt different strategies for completing the same task. The critical factor remains 'consistency', not necessarily in behaviour but in the relationship between behaviour and neural activity. In our task, monkey R exhibited responses at the 650-ms CTOA typical of cued-response tasks (e.g., Posner, 1980): faster

responses to cued locations and slowed responses to targets that unexpectedly appeared at the uncued location. By contrast, monkey O showed an opposite-side advantage at both CTOAs, suggesting that this monkey was not using the cue's position to guide future responses. These distinct behavioural strategies were associated with two different neural correlates that were absent when the behaviours were not observed.

Inhibition of return linked with decrease in target-aligned activity in dSC

IOR refers to the tendency to orient faster towards novel locations than previously attended ones (Posner et al., 1985). IOR can be composed of two independent behavioural effects: inhibited responses to previously attended locations ('same-side disadvantage') and facilitated responses to novel locations ('opposite-side advantage'; Bell et al., 2004; Bennett & Pratt, 2001; Pratt & Abrams, 1999). The IOR observed in the current study (Fig. 1) was strongly correlated with a reduction in the magnitude of the target-aligned response in the SC (Figs 2 and 3), which is consistent with what has been observed previously for nonpredictive cued-saccade tasks (Dorris et al., 2002; Bell et al., 2004; Fecteau et al., 2004).

A hypothetical mechanism linking reduced target-aligned activity with SRT has been described elsewhere (see Bell *et al.*, 2004; Fecteau *et al.*, 2004 for details). Briefly, following the initial phasic response to the visual or audiovisual cue there is a steady increase in activity leading up to target onset. When the target appears, the corresponding target-aligned response is reduced compared to the Invalid condition. The reduced activity provides a lower baseline upon which the premotor activity can build. Thus, additional time is required to surpass saccadic threshold, resulting in a longer SRT. When the cue appears outside the response field of the neuron (Invalid condition), there is believed to be a transient suppression of the ipsilateral SC (Everling *et al.*, 1998; Dorris *et al.*, 2007). Once the target appears, however, a postinhibitory rebound of the neural activity (Okada *et al.*, 1990; Syed *et al.*, 1990; Nishimura *et al.*, 1992) has been hypothesized (Bell *et al.*, 2004); this results in a stronger target-aligned response. This enhanced response could potentially give rise to the opposite-side advantage characteristic of the 'facilitation to novel locations' component of IOR mentioned above.

Note that both the reduced target-aligned response driving a same-side disadvantage and the post-inhibitory rebound driving an opposite-side advantage are believed to be mediated by bottom-up, involuntary mechanisms (see Bell *et al.*, 2004; Fecteau *et al.*, 2004). This is supported by the observation that both monkeys exhibited this behaviour, including monkey R who, based on his performance at the 650-ms CTOA, understood the predictive nature of the cue. The benefit of the cue, which would presumably drive a same-side advantage, was masked by the reflexive consequences of initially orienting towards the cue, which produce IOR at this early CTOA.

How do increases in pretarget activity lead to the behavioural effects observed in monkey R? Similar to IOR, attentional facilitation can reflect the sum of two different processes: facilitated responses to the cued location and inhibited responses to the uncued location. In the case of former, we propose that the following two mechanisms may be involved. First, the increase in pretarget activity partially restores the reduced target-aligned response that typically follows the repeated stimulation of a neuron's response field (e.g., Fig. 2; see also Fecteau *et al.*, 2004), elevating the baseline activity for incoming target signals thus facilitating the triggering of shorter-latency saccades. Second, increases in the activity of sensory–motor neurons in the caudal dSC can lead to a reduction in fixation-related activity, which normally serves to suppress unwanted movements (see Munoz & Fecteau, 2002; Sparks, 2002 for review). This would further facilitate the generation of shorter latency saccades by releasing local and downstream inhibition (Everling *et al.*, 1998; Sparks, 2002; Trappenberg *et al.*, 2001).

In the case of inhibited responses to the uncued location, activity within the dSC contralateral to the cue could lead to inhibition of the ipsilateral dSC. This could be mediated locally, via lateral inhibitory projections (Munoz & Istvan, 1998; Olivier *et al.*, 2000), and/or via top-down signals from cortical structures. The latter could potentially account for the slowed responses to the uncued location in cued-response tasks. When the target does not appear at the cued location and the monkey must generate a saccade to the uncued location, neurons responsible for generating the saccade (i.e. those ipsilateral to the cue) must overcome this inhibition before a saccade can be triggered, requiring additional time relative to saccades generated to a cued or neutral location.

Attentional facilitation linked with increase in pretarget activity in dSC

The most striking discrepancy between the two monkeys was the significant pretarget activity following cue presentation at the 650-ms CTOA observed in monkey R but not monkey O (Figs 2 and 3). Previous studies have connected increases in pretarget activity in the dSC with top-down modulation (Dorris *et al.*, 2002; Fecteau *et al.*, 2004; Ignashchenkova *et al.*, 2004), which may represent a physiological basis for the microstimulation studies implicating the dSC in covert attention (Kustov & Robinson, 1996; Muller *et al.*, 2005). Our data build upon these previous studies by showing that the absence of this activity is correlated with a lack of behavioural effect, linking pretarget activity in this task with attentional facilitation. This critical distinction is necessary for evaluating relationships between neural activity and behaviour (Parker & Newsome, 1998). Without this negative control it would be difficult to conclude that this activity is not, for example, sensory activity related to the cue or indiscriminate motor preparation driven by bottom-up processes, both of which are observed in the dSC (Sparks & Hartwich-Young, 1989; Dorris & Munoz, 1998).

A correlation between pretarget activity and SRT has been demonstrated quite convincingly in a number of previous studies (e.g., Basso & Wurtz, 1997, 1998; Dorris & Munoz, 1998). Surprisingly, the correlation between pretarget activity and SRT in the current study was weak. This may reflect significant differences in task between the aforementioned studies and the current one and/or the significant differences in behaviour across the two monkeys. Nonetheless, there was a strong relationship between pretarget and target-aligned activity, suggestive of at least an indirect relationship between pretarget activity and SRT.

Interactions between top-down and bottom-up control of shifts in attention

An important factor in our task that influenced behaviour and neural responses was CTOA. At the 250-ms CTOA, both monkeys displayed behaviour consistent with bottom-up-mediated IOR (Bell *et al.*, 2004; Fecteau *et al.*, 2004) whereas at the 650-ms CTOA, the monkeys showed evidence of differential involvement of bottom-up vs. top-down processes. This result shows how bottom-up and top-down control mechanisms can interact in a time-dependent fashion. In the case of monkey R, while increases in pretarget activity mediated by top-down processes may serve to facilitate responses to the cued location, they were insufficient at the 250-ms CTOA to overcome the more powerful bottom-up processes that favoured responses to the uncued location (see also Fecteau *et al.*, 2004). When the CTOA was increased to 650 ms, however, the bottom-up-mediated reduction in the target-aligned response was less and the pretarget activity was greater such that a partial (as seen in Fecteau *et al.*, 2004) or complete reversal in behaviour could occur. Monkey O did not show any evidence of a top-down-mediated increase in pretarget activity or a reversal in behaviour at the 650-ms CTOA. In the absence of any competing top-down influences, one would predict that bottom-up or 'involuntary' mechanisms should continue to drive behaviour.

What is driving these increases in pretarget activity? The intermediate layers of the SC receive numerous projections from cortical structures, many of which are in an ideal position to affect changes in behaviour related to shifts in attention. For example, Bisley & Goldberg (2003a) found similar patterns of activity in neurons in the lateral intraparietal sulcus (LIP). Following cue onset, neurons in LIP show a low-level, tonic discharge preceding target onset. Moore & Fallah (2004) have shown that stimulating the frontal eye fields (FEF)

improved monkeys' ability to detect changes in luminance, an improvement commonly associated with covert attention. Both LIP and FEF project directly to the dSC (Kunzle *et al.*, 1976; Paré & Wurtz, 1997), both have been implicated in spatial attention (Goldberg *et al.*, 2002; Bisley & Goldberg, 2003b; Moore *et al.*, 2003; Moore & Fallah, 2004) and, finally, together these three structures have complementary functions in the generation of internally and externally driven motor plans (Bisley & Goldberg, 2003a; Munoz & Schall, 2004; Schall, 2004). Further study is necessary to identify the functional relationship between activities in cortical vs. subcortical structures related to covert attention. Nonetheless, these results stress the ubiquitous nature of these signals throughout the brain, suggesting that the control and maintenance of attention is a distributed process as opposed to being localized to a single structure (Kim *et al.*, 1999; Nobre *et al.*, 2000; Corbetta & Shulman, 2002; Gitelman *et al.*, 2002; Shulman *et al.*, 2002).

Conclusions

We have taken advantage of differences in behavioural strategy to investigate the role of the dSC in covert shifts in attention. Our data illustrate how bottom-up and top-down processing can compete within a single task to drive behaviour in opposite directions. Using the information provided by the cue shifts the emphasis towards top-down processing, resulting in attentional facilitation. Ignoring the predictive nature of the cue allows bottom-up processing to continue to dominate. Regardless of the selected strategy, however, neurons in the dSC consistently reflected the current bias between the two processes, emphasizing its role in both the bottom-up and top-down control of covert orienting.

Acknowledgements

Abbreviations

CTOA, cue–target onset asynchrony; dSC, intermediate and deep layers of the SC; IOR, inhibition of return; SC, superior colliculus; SRT, saccadic reaction time.

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