The Influence of Stimulus Properties on Mutisensory Processing in the Awake Primate Superior Colliculus

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Abstract Multisensory integration is a process whereby information converges from different sensory modalities to produce a response that is different from that elicited by the individual modalities presented alone. A neural basis for multisensory integration has been identified within a variety of brain regions, but the most thoroughly examined model has been that of the superior colliculus (SC). Multisensory processing in the SC of anaesthetized animals has been shown to be dependent on the physical parameters of the individual stimuli presented (e.g., intensity, direction, velocity) as well as their spatial relationship. However, it is unknown whether these stimulus features are important, or evident, in the awake behaving animal. To address this question, we evaluated the influence of physical properties of sensory stimuli (visual intensity, direction, and velocity; auditory intensity and location) on sensory activity and multisensory integration of SC neurons in awake, behaving primates. Monkeys were trained to fixate a central visual fixation point while visual and/or auditory stimuli were presented in the periphery. Visual stimuli were always presented within the contralateral receptive field of the neuron whereas auditory stimuli were presented at either ipsi- or contralateral locations. Many of the SC neurons responsive to these sensory stimuli (n = 66/84; 76%) had stronger responses when the visual and auditory stimuli were combined at contralateral locations than when the auditory stimulus was located on the ipsilateral side. This trend was significant across the population of auditory-responsive neurons. In addition, some SC neurons (n = 31) were presented a battery of tests in which the quality of one stimulus of a pair was systematically manipulated. A small proportion of these neurons (n = 8/31; 26%) showed preferential responses to stimuli with specific physical properties, and these preferences were not significantly altered when multisensory stimulus combinations were presented. These data demonstrate that multisensory processing in the awake behaving primate is influenced by the spatial congruency of the stimuli as well as their individual physical properties.

Résumé L'intégration multisensorielle est un processus par l'entremise duquel l'information qui converge des différentes modalités sensorielles en vient à produire une réponse différente de celle déclanché par chacune des modalités prises individuellement. Une possible base neurologique de l'intégration multisensorielle a été identifiée dans de nombreuses régions du cerveau, mais le modèle le plus complètement étudié identifie le colliculus supérieur (CS) comme siège de l'intégration multisensorielle. Le traitment multisensoriel qui s'opère dans le CS chez des animaux sous anesthésie s'est révélé tributaire des propriétés physiques des stimuli individuels présentée (p. ex., intensité, direction et vitesse), tout comme de leurs relations spatiales. Toutefois, on ignore si ces caractéristiques des stimuli ont de l'importance, ou encore sont évidentes, pour un animal éveillé et fonctionnel. Afin d'étudier cette question, nous avons évalué l'impact des propriétés physiques de stimuli sensoriels (intensité, direction et vitesse visuelles; intensité et site auditifs) sur l'activité sensorielle et l'intégration multisensorielle des neurones du CS chez des primates éveillés et fonctionnels. Nous avons entraîné des singes à fixer un point visuel central pendant que des stimuli visuels, auditifs, ou des deux types, était eut présentés en périphérie. Les stimuli visuels étaient toujours présentés dans le champ récepteur controlatéral du neurone, tandis que les stimuli auditifs étaient présentés dans des sites épsilatéraux et controlatéraux. De nombreux neurones du CS répondant à ces stimuli sensoriels (n = 66/84; 76 %) ils faisaient de façon plus marquée lorsque les stimuli visuel et auditif étaient combinés aux sites controlatéraux que lorsque le stimulus auditif était placé épsilatéralement. Cette tendance était significative pour l'ensemble des neurones répondant aux stimuli auditifs. De plus, certains des neurones du CS (n = 31) ont été soumis à une batterie de tests lors desquels la qualité d'un stimulus faisant partie d'une paire était systématiquement manipulée. Une petite proportion de ces neurones (n = 8/31; 26 %) a produit des réponses préférentielles aux stimuli possédant des attributs physiques précis, et ces préférences n'étaient pas significativement modifiées

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lorsque les combinaisons de stimuli multisensoriels étaient présentées. De telles données révèlent que le processus multisensoriel chez le primate éveillé et fonctionnel dépend de la congruence spatiale des stimuli, de même qui de leurs caractéristiques physiques particulières.

It is well known that the presence of a stimulus from one sensory modality can influence the processing of a stimulus from another (see Stein & Meredith, 1993, for a review). For example, saccades made to combined visual and auditory targets have shorter reaction times than saccades to unimodal visual or auditory targets (Corneil and Munoz, 1996; Harrington & Peck, 1998; Hughes et al., 1994). Furthermore, Corneil and colleagues (2001) have shown that humans are better able to localize a visual target in a complex sensory environment if it is paired with a subthreshold auditory cue. For this to occur, inputs from different sensory modalities must converge onto single neurons or structures. This is known to occur in a number of brain areas but is perhaps best understood within the superior colliculus (sc; see Stein & Meredith, 1993 for a review).

Neurons in the intermediate and deep layers of the sc receive convergent sensory inputs for different modalities (e.g., visual, auditory, somatosensory; Cynader & Berman, 1972; Groh and Sparks 1996; Jay & Sparks, 1984; Updyke, 1974) and play a critical role in the execution of orienting responses (see Munoz et al., 2000, for a review). Not only do sc neurons dramatically increase their firing rates when two stimuli of different modalities are combined (compared to when the stimuli were presented independently; Meredith & Stein, 1986), but these same neurons project to the brain stem premotor circuitry for movements of the eye, head, and pinnae (Meredith et al., 1992; Meredith & Stein, 1995).

The majority of investigations of multisensory integration in the sc have used anaesthetized animal preparations, primarily the cat (see Stein & Meredith, 1993, for a review), ostensibly to minimize the influence of movement related activity or behavioural states. These studies showed that multisensory integration in the anaesthetized animal is dependent on several stimulus-related properties, such as their physical attributes (e.g., intensity, velocity, direction of motion; Meredith & Stein, 1986a; Wallace et al., 1996). Likewise, the spatial and temporal relationship of the two or more stimuli being presented had a strong influence on the resulting interactions (Meredith et al., 1987; Meredith & Stein 1986b; Meredith & Stein, 1996). When the stimuli were presented close in time and space, interactions were strongest. As the distance or timing between the two stimuli was increased, interactions became weaker.

More recently, studies in awake animals have identified nonstimulus-related, behavioural parameters that also affect multisensory integration. For example, Frens and Van Opstal (1998) observed that if combined visual-auditory stimuli are the target for an impending saccade, the discharge rates of the saccade-related neurons in the sc are significantly increased compared to a unimodal visual target. Bell and colleagues (2000) have also demonstrated that fixation of a central visual stimulus suppresses sensory responses to peripheral visual and/or auditory stimuli and decreases the probability of eliciting multisensory interactions compared to if the animal is fixating a virtual spot in space in the absence of an exogenous cue. Neither of these behavioural influences on multisensory integration could have been tested in anaesthetized preparations. However, like anaesthetized preparations, recent data from the sc of unanaesthetized cats confirms that sc neurons integrate multisensory information and that the spatial arrangement of the stimuli is still important (Wallace et al., 1998). The objective of the present study is to extend these observations to the alert, behaving monkey and to examine the influence of several physical parameters of sensory stimuli as well as their spatial congruency on multisensory integration in the sc. Preliminary results have been presented in abstract form (Belle et al., 2000).

Method

PREPARATION OF EXPERIMENTAL ANIMALS

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*), weighing 6 and 8 kg, were used in this study. Animals were prepared for chronic experiments in one surgical session conducted under Ketamine/Halothane anaesthetic under aseptic conditions (see Munoz & Istvan, 1998, for details). Scleral search coils to monitor eye position and a head restraint device were implanted. A stainless steel recording chamber, centred on the midline and tilted 38° posterior of vertical, was implanted to allow recordings from both superior colliculi. Animals were given a course of antibiotic and analgesic treatment and monitored closely following surgery. They were allowed a recovery period of at least two weeks prior to initiation of behavioural training.

PROCEDURES

The experiments took place in a dark, sound-attenuated room. The animals were seated in a primate chair with their heads restrained 94 cm from a translucent tangent screen spanning approximately ±45° of the visual field. The monkeys were trained to fixate a laser-generated central fixation point (FP; 8.4 cd/m^2) back-projected onto the tangent screen while irrelevant visual and/or auditory stimuli were presented in the periphery. These stimuli were defined as irrelevant in that they did not serve as a target for a gaze shift and the monkey was not required to attend to them in any way. The irrelevant visual stimuli consisted of moving rectangular bars of white light of preset size (subtending 0.5-5.0° of visual angle) and intensity (2.2-5.0 cd/m^2) generated by a slide projector and ultimately projected against the tangent screen. They were projected onto a galvanometer-driven mirror that smoothly displaced the stimulus from one extent of the visual receptive field to the other at a preset velocity ranging from 50-400°/s with an amplitude between 10 and 20°. The stimuli were then reflected through a rotating prism and onto a second mirror to affect changes in orientation and location of the stimulus. The irrelevant auditory stimuli consisted of white noise (100 ms duration, 40-80 dB, SPL, A-scale), produced by small (4 cm) 8.0Ω speakers suspended in a fixed position in front of the tangent screen, facing the animal.

RECORDING TECHNIQUES

The techniques used to record single neuron activity in both SC were described previously (Munoz & Istvan, 1998). Single-neuron activity was sampled at 1 kHz after passing through a window discriminator, 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). Eye position was sampled at 500 Hz.

MULTISENSORY FIXATION PARADIGM

The monkeys were trained on a multisensory fixation paradigm. The onset of each trial was signaled by the removal of the background illumination and appearance of the central FP which the animal was required to fixate for a period of 800-1,500 ms. The FP then disappeared for 310 ms before reappearing, during which time the irrelevant visual and/or auditory stimuli were presented. The irrelevant stimuli appeared 150 ms (visual) and 190 ms (auditory) after the FP disappeared. The 40-ms asynchrony between the presentation of the visual and auditory stimuli corresponds roughly to differences in central response latencies to visual and auditory stimuli (Gouras, 1967; Kraus & McGee, 1992). This offset was introduced in order to increase the probability of the two responses occurring simultaneously within the SC and thus maximize the potential interactions between the visual and auditory stimuli (Meredith et al., 1987). The irrelevant visual stimulus was presented within the centre of the neuron's visual receptive field. The location of the receptive field was estimated by sweeping a bar of light generated by a hand-held ophthalmoscope while the animal fixated the FP. Because previous studies have shown that auditory receptive fields in the SC tend to be very large (45-180° in diameter in the contralateral hemifield in anaesthetized primate, Wallace et al., 1996), no attempt was made to align the auditory stimuli within the receptive field. Instead, one auditory stimuli was placed in proximity to the visual stimulus, separated by an average of 14±9° (0-36°). In addition, because some neurons respond to auditory stimuli located both ipsi- and contralateral to the recording site (Wallace et al. 1996), a second speaker was positioned in the ipsilateral field. The stimuli were presented randomly interleaved in the following distribution: 17% visual stimulus only, 33% auditory stimulus only (16.5% contralateral, 16.5% ipsilateral), 33% combined visual-auditory stimuli (16.5% auditory stimulus contralateral, 16.5% auditory stimulus ipsilateral), 17% no stimuli ("catch trials"). Monkeys received a liquid reward if they maintained fixation (i.e., kept their eyes within a 2° window surrounding the FP) for the duration of the trial without orienting to the irrelevant stimuli. They worked until fully satiated, at which point they were returned to their home cages.

DATA ANALYSIS

All data analysis was carried out on a Sun Ultra 60 Sparcstation with user-generated programs and a Pentium PC running MatLab software (Mathworks Inc.). Prior to analysis, any incorrect (i.e., monkey generated eye movements) or inappropriate (e.g., poor single neuron isolation) trials were rejected. Sensory responses were analyzed by constructing a spike density function for each response based on a poisson distribution. Each spike in a given trial was convolved with the following function (Thompson et al., 1996)

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

where the activation level A as a function of t varies 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. This spike density function was used to determine the peak response density, used as the measure for response quantification. Statistical significance across conditions within individual neurons and across

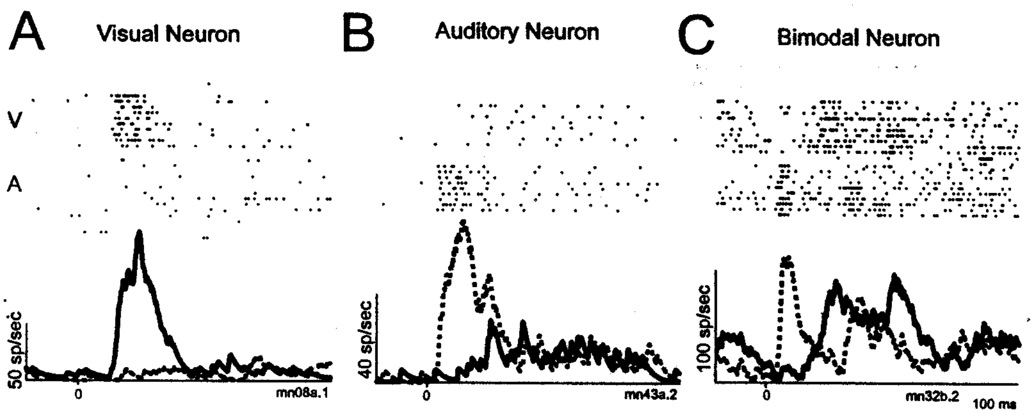

Figure 1. Spike density functions and raster displays of the visual (solid line) and contralateral auditory (dashed line) responses in the SC. **A:** Neuron responding only to the visual stimulus. **B:** Neuron responding only to the auditory stimulus. **C:** A bimodal neuron responding to the individual presentation of both the visual and auditory stimuli.

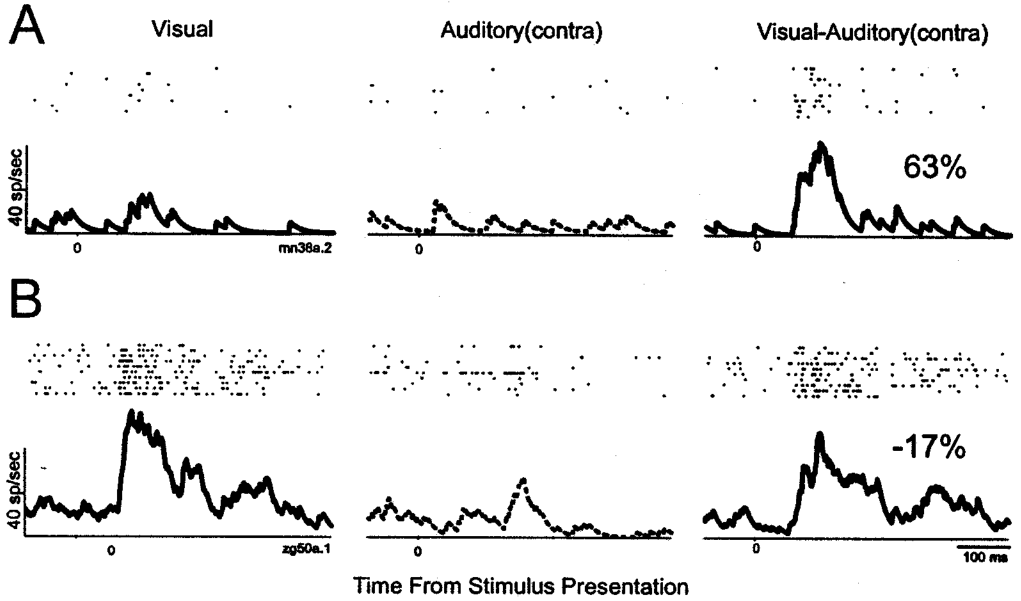

Figure 2. Examples of multisensory interactions in SC neurons. **A:** Example of a neuron showing significant response enhancement. **B:** Example of a neuron showing significant response depression.

the population was evaluated using a Wilcoxon Rank Sum Test ($p < 0.05$). A Kruskal-Wallis Test was used to evaluate the effect of stimulus parameters on response magnitude ($p < 0.05$).

Results

A total of 84 neurons were recorded in the SC of two monkeys (43 from monkey A, 41 from monkey B). Similar results were obtained from both monkeys and thus all results were grouped across both monkeys. Of these neurons, 66 (76%) displayed changes in activity correlated with the presentation of visual and/or auditory stimuli while the animal maintained central fixation. The basic response properties of SC neurons in this condition have been reported elsewhere (Bell et al., 2001). Briefly, neurons in the SC were classified as visual (Figure 1A), auditory (Figure 1B), or bimodal (i.e., responsive to individual presentation of visual and auditory stimuli; Figure 1C) based on their responsiveness to the different stimuli. When the visual and auditory stimuli were combined in a single trial, a number of neurons showed either response enhancement (12/66; 18%; Figure 2A), wherein the peak response to combined visual-auditory stimulation was significantly greater than the strongest unimodal response, or response depression (4/66; 6%; Figure 2B), wherein the combined response was significantly weaker than the strongest unimodal response.

EFFECT OF AUDITORY STIMULUS LOCATION

To examine the influence of stimulus location on sensory activity in awake primates, the visual and auditory stimuli were presented in one of two spatial arrangements for a large proportion of the sensory-related neurons examined (54/66; 84%). The visual stimulus was always swept through the visual receptive field (i.e., in contralateral visual space) and the auditory stimulus was located either 30° contralateral (i.e., same side as visual stimulus) or ipsilateral to the side of the recording site. Of the 54 neurons tested using combined stimuli in these two spatial conditions, 13 (24%) displayed a significant multisensory interaction (i.e., 10 neurons showing response enhancement; 3 neurons showing response depression; $p < 0.05$; Wilcoxon Rank Sum Test). These neurons included visual (6), auditory (1), and bimodal (5) neurons as well as one which showed no unimodal responses. Many of the neurons that responded with significant response enhancement (7/10; 70%) did so only when the visual and auditory stimuli were both located in contralateral visual space, an example of which is shown in Figure 3A. Similarly, the majority of neurons that displayed response depression (2/3; 67%) did so only when the visual stimulus was located contralateral and the auditory stimulus located ipsilateral. Curiously, the remaining four neurons showing multisensory integration showed the reverse effects. Three featured response enhancement when the stimuli were located on opposite sides of the midline, and one featured response depression with both combined stimulus arrangements. An analysis of the auditory-responsive neurons (i.e., auditory and bimodal neurons) showed that this trend of increased responsiveness to contralateral auditory stimuli was significant for the population ($p < 0.05$; Wilcoxon Rank Sum Test; Figure 3B). This trend was not significant for visual neurons ($p < 0.50$; Wilcoxon Rank Sum Test; not shown).

EFFECT OF STIMULUS PARAMETERS ON MULTISENSORY PROCESSING

To determine the interaction between stimulus parameters and the sensory activity and multisensory processing of SC neurons in awake primates, the sensory activity of a total of 31 neurons was examined in response to systematic (2-4 steps) changes in the physical quality of a stimulus presented alone and in combination with a stimulus from another modality. We manipulated visual stimulus intensity (2.2 to 5.0 cd/m2), direction of visual stimulus movement (nasal to temporal – 0°, temporal to nasal – 180°, inferior to superior – 90°, and superior to inferior – 270°), velocity of visual stimulus movement (50-400 deg/s), and auditory stimulus intensity (from 41-77 dB, SPL, A-scale).

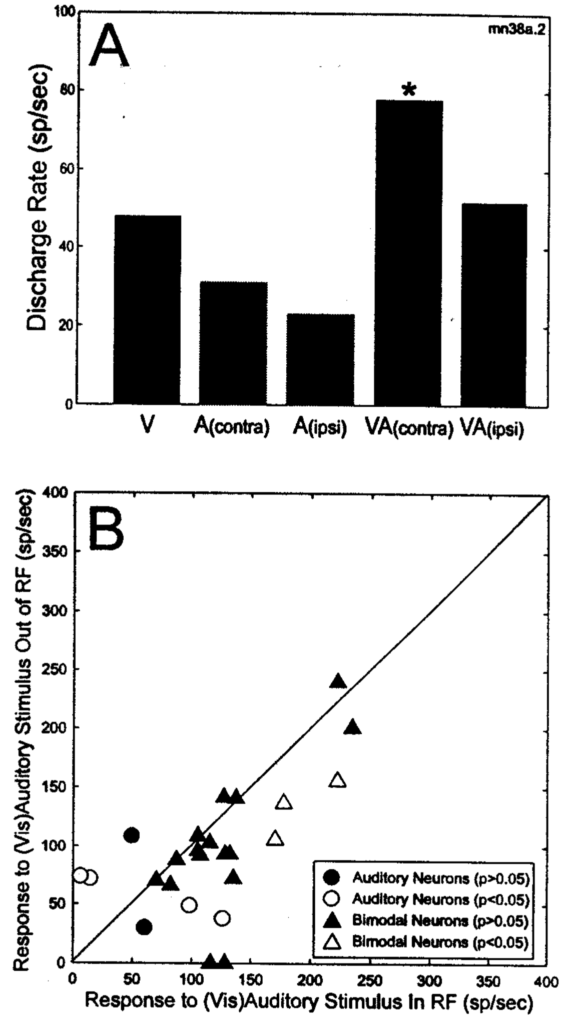

Figure 3. The influence of auditory stimulus location on sensory activity in the SC. **A.** Example of a neuron showing significant multisensory enhancement only when the auditory stimulus is located in the contralateral side ($p < 0.05$; Wilcoxon Rank Sum Test), indicated by an asterix. **B.** Population analysis for spatial dependence of auditory-responsive neurons in the SC. Auditory neurons shown as circles; bimodal (neurons responding to individual presentation of both visual and auditory stimuli) shown as triangles. Significant effects ($p < 0.05$; Wilcoxon Rank-Sum Test) are shown as hollow circles/triangles.

Of these neurons, only 26% (8/31) were shown to be sensitive to one or more of the individual stimulus properties. These neurons appeared to be selectively tuned for a given stimulus setting which, when present-

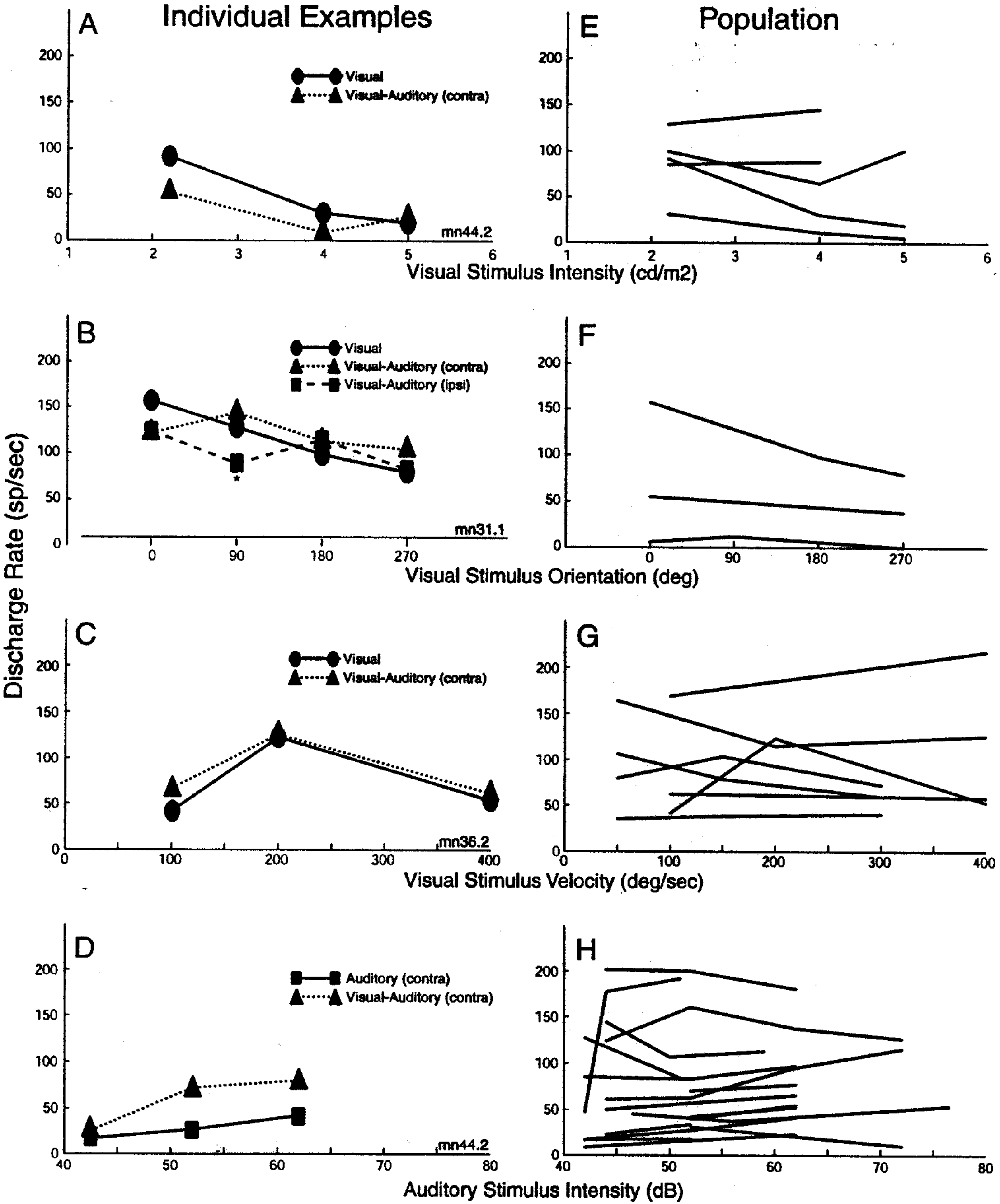

Figure 4. The influence of the stimulus properties on sensory activity in the sc in individual neurons (A-D) and across the population (E-H). **A:** Neuron showing a significant effect of visual stimulus intensity on its unimodal and combined (contra) response magnitudes ($p < 0.05$; Kruskal-Wallis). **B:** Neuron showing a significant effect of the direction of visual motion on its unimodal and combined (ipsi only) response magnitudes ($p < 0.05$; Kruskal-Wallis). A significant response depression is indicated by the asterix ($p < 0.05$; Wilcoxon Rank Sum Test). **C:** Neuron showing a significant effect of the velocity of visual motion on its stimulus intensity on its unimodal and combined (contra) response magnitudes ($p < 0.05$; Kruskal-Wallis). **D:** Neuron showing a significant effect of auditory stimulus intensity on its combined (contra) response magnitude ($p < 0.05$; Kruskal-Wallis). **E-G:** Unimodal visual responses for the sample populations of neurons tested with different visual stimulus properties. **H:** Unimodal auditory (contra) responses for the sample population of neurons tested with different auditory intensities.

ed, elicited maximal responses. For example, of the five neurons presented with different visual stimulus intensities, two showed a significant change in their unimodal response, an example of which is shown in Figure 4A where the response was strongest when the visual stimulus intensity was weakest, indicating that high contrast levels were not required for maximal activation. There was no consistent trend for the unimodal responses across the sample of neurons tested (Figure 4E). Of the three neurons tested with visual stimuli presented in each of the four directions of movement, one showed preferential responses to a stimulus moving in the nasal-temporal direction and reduced activity for movement in the opposite direction (see Figure 4B; $p < 0.01$; Kruskal-Wallis). The remaining two neurons showed no selectivity at all (Figure 4F). Two of seven neurons showed a preference for visual stimulus velocity, revealing maximal responses to stimuli delivered at 200 deg/s while exhibiting significantly less activity to visual stimuli at faster or slower speeds (Figure 4C; $p < 0.05$; Kruskal-Wallis). Note that one of these neurons was also selective for visual stimulus intensity and is shown in Figure 4A. There was no visible trend, however, for the sample population (Figure 4G). Finally, 4 of 16 neurons showed systematic response changes corresponding to changes in auditory stimulus intensity. Figure 4D illustrates the activity of a neuron whose responses increase with increasing stimulus intensity. There was, however, substantial variability across the population (Figure 4H). Each of these unimodal response properties was not unexpected, and they largely correspond with those identified in SC neurons of anaesthetized animals.

Evidence from anaesthetized animals also indicates that response preferences identified using unimodal stimuli remain effective, albeit in an augmented fashion, when a second stimulus of a different modality is added. These observations were confirmed here in awake, behaving primates. For example, the sensitivity of the neuron depicted in Figure 4A to visual stimulus intensity remained unchanged when an auditory stimulus was also present. Similarly, response properties such as visual stimulus direction selectivity (Figure 4B), visual velocity selectivity (Figure 4C), and auditory stimulus intensity preferences (Figure 4D) remained unchanged when in the presence of a stimulus from another modality. With respect to multisensory interactions, there were a few different trends apparent. For example, the neuron shown in Figure 4B showed a significant response depression with the auditory stimulus located in the ipsilateral field, when the visual stimulus was moving inferior-superior (90°; $p < 0.05$; Wilcoxon Rank Sum Test) with no multisensory interactions with other stimulus orientations or configurations. In addition, two neurons selective for visual stimulus velocity experienced a change in their multisensory processing with changes in the velocity of the visual stimulus. These two neurons featured response enhancements when the velocity of the visual stimulus was least effective at eliciting a unimodal response ("inverse effectiveness"; $p < 0.05$; Wilcoxon Rank Sum Test).

Discussion

In this study, we have confirmed that the influence of spatial congruency and stimulus parameters (i.e., visual stimulus intensity, direction, velocity, and auditory intensity), factors previously shown to affect multisensory integration in anaesthetized preparations (Meredith & Stein, 1986a; Wallace et al., 1996), can also have an effect on neural processing in the awake, behaving animal. The sensory activity and multisensory processing of neurons in the SC of awake primates were significantly affected by the spatial congruency of the visual and auditory stimulus. In neurons with multisensory interactions, the auditory stimulus located contralateral to the recording site most often resulted in response enhancement whereas the auditory stimulus located ipsilateral most often led to response depression, demonstrating a spatial selectivity, similar to that previously identified in anaesthetized preparations (Meredith & Stein, 1986b; Meredith & Stein 1996; Wallace et al., 1996). A much smaller proportion of neurons showed unique preferences for stimulus properties. These results demonstrate that multisensory processing in awake, behaving primates is under similar influences as identified previously in the anaesthetized preparation (Wallace et al., 1996). However, to what degree these influences affect orienting behaviour is still unclear.

Multisensory integration aids in our perception of specific events when cues from a single modality would not be sufficient to alert our attention or not yield enough information. Therefore, it seems likely that cues relating to different events would not be integrated or could even inhibit each other. Based on the assumption that different cues from the same event will occur at the same location, we can further assume that if two cues of different modality are presented at different locations, they will be treated as relating to two separate events, and thus the likelihood they will be integrated will be reduced. This has been demonstrated in several behavioural experiments (e.g., Corneil & Munoz, 1996; Frens et al., 1995) and has been reflected at the neuronal level in our data. SC neurons demonstrating significant response enhancements were, for the most part, selective in that they would only show this enhancement if the two stimuli were both located in the contralateral field. Additionally, the population of neurons that responded to auditory stimuli (i.e., auditory and bimodal neurons) had stronger responses when the stimuli were located in the field contralateral to the recording site (Figure 3B). These results suggest that multisensory enhancements were more likely when the stimuli were spatially congruent.

When a stimulus is presented, neurons coding that location in visual space increase their activity, creating a "point image" on the SC visuomotor map (McIlwain, 1975; Munoz & Guitton, 1991). Thus, when multiple stimuli are presented, multiple point images are created. If these images overlap, as would occur if the stimuli were spatially congruent, there is a higher probability that a response enhancement will occur. However, some collicular neurons are known to exhibit ipsilateral inhibitory regions. Thus, if the two images do not overlap or are located in opposite hemifields, as was the case in our study, an inhibition can occur (Kadunce et al., 1997; Meredith & Stein, 1986b; Meredith & Stein, 1996; Rizzolatti et al., 1973), likely mediated by lateral inhibitory interconnections within and between the colliculi (Meredith & Ramoa 1998; Munoz & Istvan, 1998; Olivier et al., 1999). Other studies in the SC have demonstrated that there is, in fact, a continuum wherein the closer two different stimuli are to each other, the stronger the neuronal responses, the greater the probability and magnitude of multisensory integration (Meredith & Stein, 1986b; Meredith & Stein, 1996), and consequently the greater the behavioural benefit (Frens et al., 1995).

Some of the neurons examined did not appear to follow this general spatial principle: there were occasional examples of disparate multisensory stimuli evoking response enhancement, and others where congruous stimuli elicited response depression. In these cases, however, because the auditory receptive fields could not be mapped, the receptive field basis for these "anomalous" interactions could not be determined. Nevertheless, it is important to note that multisensory neurons with misaligned receptive fields have been reported in the macaque SC (Wallace et al., 1996), a configuration in which congruent stimuli produce response depression and incongruent stimuli produce response enhancement. As these authors reported, the functional or behavioural role of these interactions remains enigmatic.

The present study also confirmed the presence of sensory response preferences in SC neurons of the awake, behaving primate. In and of itself, this is not unexpected. It is a fundamental property of sensory neurons to respond preferentially to a specific stimulus quality. What is surprising is the small proportion of neurons that exhibited distinct response preferences. Less than half of all neurons tested for any parameters (intensity, velocity, direction) showed significant response changes that corresponded with changes in the quality of the stimulus. However, the primate SC contains a lower proportion of neurons with distinct response properties than identified in other specifies, such as the cat (Wallace & Stein, 1996). Thus the reduced sensory tuning in this species and the small sample size may account for the character of the present sample.

In the awake, behaving primate, the modality-specific response properties of SC neurons also influenced the outcome of multisensory interactions. Neurons that showed velocity, intensity, or directional preferences in one modality, in general, maintained these preferences in the presence of a stimulus from another modality. This general trend corresponds with that reported in anaesthetized animals (Meredith & Stein 1986a; Stein et al., 1993) and it is important because it indicates, at least for enhanced responses, that multisensory processing does not disrupt established, within-modality features. Thus a neuron that exhibits directional selectivity can have its response enhanced by the presence of an appropriate stimulus from another modality.

SC and cortical neurons in anaesthetized animals as well as multisensory behavioural performance (Meredith & Stein, 1986a; Wallace et al., 1993; Wallace et al., 1996) have been shown to demonstrate an "inverse effectiveness" phenomenon. Stated simply, the least effective stimuli are most likely to yield the greatest proportional change in activity when combined. Conversely, stimuli that are highly effective individually exhibit little response increment when a stimulus from a second modality is added. While this effect was evident in some cases, this trend was not consistent in our data and some neurons appeared to violate this principle. In some cases, such as the neuron shown in Figure 4A, it was the *most* effective stimulus (which happened to be the weakest intensity tested) yielded the strongest combined response. One possible explanation could relate to how multisensory processing is used in a behavioural context. For example, the location of the stimuli relative to the animal's fovea may influence the strength of the response and the need for a response enhancement, as if response enhancement becomes more relevant for progressively more eccentric stimuli. This idea has recently been suggested in a model of multisensory processing in the SC (Anastasio et al., 2000). Therefore, inverse effectiveness may not have been as apparent in our data compared with previous studies because the majority of our visual stimuli were located within 20° of the centre of fixation.

Our results, therefore, demonstrate that multisensory processing in the awake, behaving primate is affected by the spatial relationships between the stimuli present-

ed, as well as their individual stimulus preferences. Future investigations will be aimed at examining how these factors are coordinated to influence behaviour of awake animals.

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