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RESEARCH NOTE

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Neuronal representation of disappearing and hidden objects in temporal cortex of the macaque

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Abstract Neurons in the anterior regions of the banks of the superior temporal sulcus (STSa) of the macaque monkey respond to the sight of biologically significant stimuli such as faces, bodies and their motion. In this study the responses of STSa neurons were recorded during the gradual occlusion of the experimenter and other mobile objects behind screens at distances of 0.5–4 m from the monkeys. The experimenter or other object remained out of sight for 3–15 s before emerging back in to view. We describe a population of neurons (n=33) showing increased activity during the occlusion of objects that was maintained for up to 11 s following complete occlusion (when only the occluder itself was visible). This increase in activity was selective for the position of the occlusion within the testing room. Many neurons showed little or no change in activity prior to occlusion when the object or experimenter was completely in view. By coding for the presence and location of recently occluded objects, these responses may contribute to the perceptual capacity for object permanence.

Keywords Macaque monkey · Object permanence · High-level visual processing · Superior temporal sulcus · Ventral stream

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Introduction

"Existence constancy" (Bower 1967) or "object permanence" (Baillargeon 1993), "the experience that objects persist through space and time despite the fact that their presence in the visual field may be discontinuous" (Butterworth 1991), has been studied behaviourally in many species. Adult birds, cats, dogs and non-human primates all exhibit object permanence (for review, see Doré and Dumas 1987). At a basic level, adults of all these species will search for an object that has recently become occluded from sight. Such behaviour is evident neither in the young of these animals nor in human infants (for reviews, see Bower 1982; Baillargeon 1993), and the development of object permanence has been studied extensively. The capacity for object permanence may depend on the ability to distinguish between the visual cues present on disappearance that are associated with permanent objects and those that are not (Michotte 1950). Such cues may be learned during development. For example, objects do not generally suddenly "blink off" and disappear – this is more likely to be associated with object destruction (e.g. the bursting of a bubble).

Michotte (1950) and Gibson (1979; Gibson et al. 1969) have described the visual cues that lead to object permanence. One of the most effective cues is that of gradual occlusion (produced, for example, when an object moves behind a screen). Gradual occlusion can lead to a strong impression of object permanence even when the observer knows that there is no permanent object present (Michotte 1950; Gibson et al. 1969), such as when the display is produced on a computer screen.

Despite extensive behavioural and perceptual studies of object permanence, little is known about the neural mechanisms underlying the perception of objects undergoing occlusion. In the present study, we examined the responses of neurons in the banks of the anterior superior temporal sulcus (STSa; Fig. 1a) of the macaque during and following the gradual occlusion of visual objects.

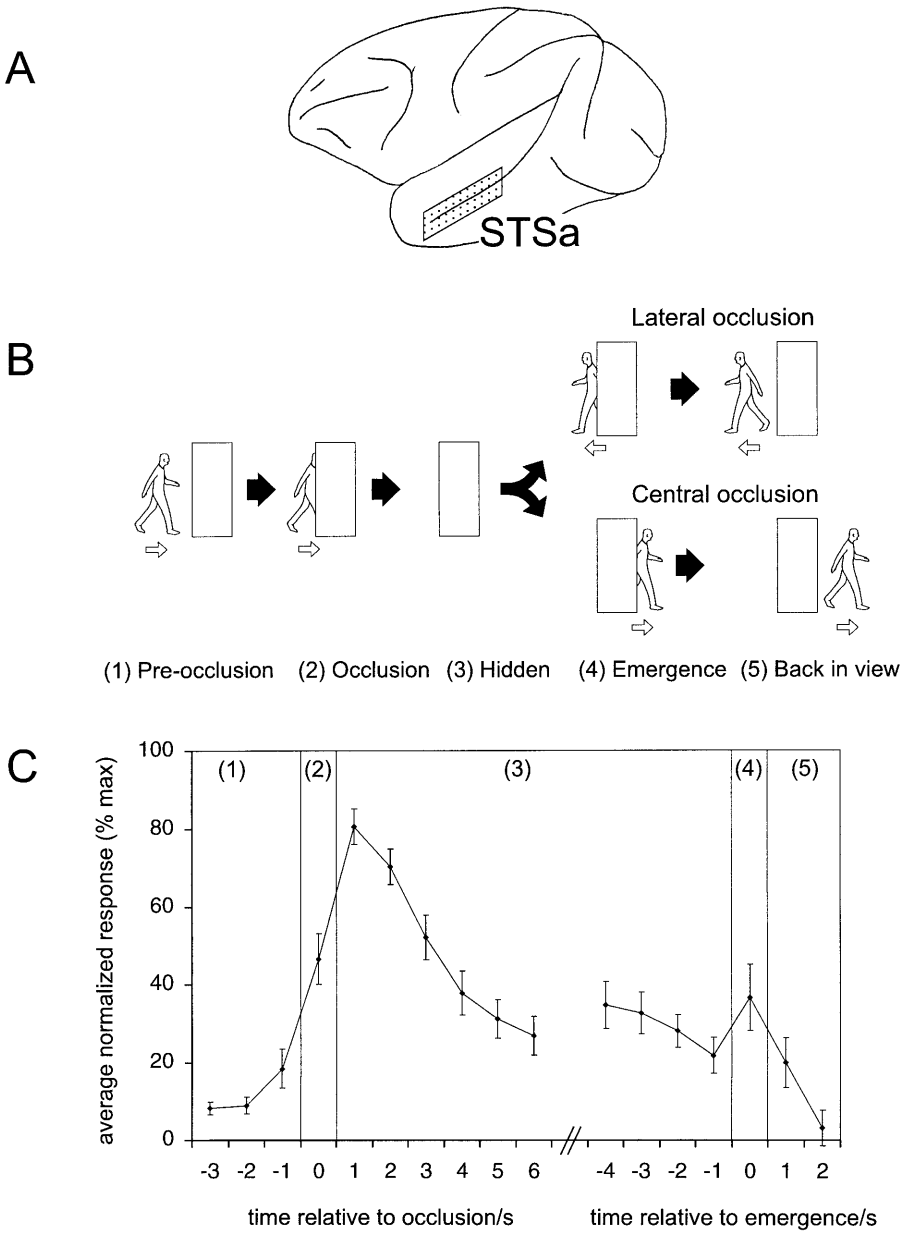

Fig. 1 **a** Recording location: 12–18 mm anterior to the interaural plane. **b** Periods of the visual stimulus. The object/experimenter moved towards the occluding screen (*1*), was gradually occluded (*2*), remained hidden from view with only the screen visible (*3*) and gradually re-emerged (*4*) until the object was once again fully in view (*5*). Emergence was in the same direction as the preceding movement for central occlusion, but in the opposite direction for lateral occlusion. *Filled arrows* show the progression of events and *outline arrows* the direction of movement. **c** Activity profile during the disappearance and subsequent emergence of the experimenter. The mean normalised population response of 26 cells recorded in anterior regions of the banks of the superior temporal sulcus (STSa). On the *left*, responses are aligned with respect to the occlusion period; on the *right*, the responses are aligned with respect to the emergence period. For each cell, there was a minimum of three trials estimating cell activity for a given time period. Activity for each cell was normalised to express the response level as a percentage of the range of activity observed in the first 3 periods of the stimulus

STSa is a cortical visual area associated with the ventral stream of visual processing, and neurons in this area have previously been shown to respond to the sight of biologically significant stimuli such as faces, bodies (Perrett et al. 1992) and their motion (e.g. walking; Perrett et al. 1989). Many of these neurons show combined sensitivity to form and motion (Oram and Perrett 1996). In this report, we describe a population of neurons that were specifically responsive to the occlusion of visual objects, with many cells showing their highest levels of activity after occlusion when only the occluding surface was visible. These neurons showed prolonged activity following occlusion and may contribute to the perceptual capacity for object permanence.

Materials and methods

Subjects and experimental set-up

The experiments were carried out on two hemispheres of two monkeys (*Macaca mulatta*, aged 4–6 years). Surgical and recording procedures have been described elsewhere (Oram and Perrett 1996). Animal care and all experimental protocols were performed in accordance with UK Home Office guidelines and followed the *Guide for the Care and Use of Laboratory Animals* (National Institutes of Health publication no. 86–23, revised 1985).

Subjects were seated in a primate chair with their head restrained. A VHS video-recorder was used to record the neural signal (audio channel) together with the visual stimulus for each trial (video channel) from the subject's perspective. The monkeys were not required to fixate due to the length of the trials (up to 25 s), but eye movements were monitored and recorded with an infrared camera (I-View; SMI, Germany). This signal was integrated (Panasonic VHS video mixer, WJAVE7) or synchronised (VITC

time-code generator and frame counter, Horita VG50) with the record of the visual stimulus.

Testing procedure

Single neurons in STSa were isolated and tested with a wide range of visual stimuli (photographs, three-dimensional objects, movements of the experimenter). Any cells showing audible change in neuronal activity to such visual stimuli were tested further. The responses of all these neurons were recorded as the experimenter walked around the testing room, went out of view behind occluding screens, and subsequently came back into view after a variable period of complete occlusion (lasting 3–20 s). The monkeys had been used in previous behavioural and physiological experiments and were used to the experimenters moving around the testing room both in and out of sight. Speed of movement was maintained across trials at approximately 0.7 m/s. The occluding screens were placed 0.5–4 m from the subject and at lateral positions up to 1.5 m from the midline of the subject. A subset of neurons were tested with the movement of other objects, chosen to be approximately the same size as the experimenter and moved around on wheels with the experimenter out of sight (e.g. an upright television stand, a chair with a tall bin on the seat). Different testing conditions (e.g. different objects, different positions of occlusion) were always tested with pseudo-randomly interleaved trials, with at least 5 trials per condition. We divided the visual stimulus into 5 distinct periods, depending on the physical relationship between the object and the screen: (1) pre-occlusion, (2) occlusion, (3) hidden (out of sight), (4) emergence, and (5) back in view (Fig. 1b).

Data analysis

Cell activity was analysed off-line in 1-s bins and aligned independently to both occlusion and emergence. Any trials in which the monkey failed to look at the stimuli were excluded from the analysis. The duration of the occlusion and emergence events (from the time the first part of the body became occluded/visible to complete occlusion/visibility) was approximately 0.5 s. Mean cell responses were analysed using repeated-measures ANOVA with time as a factor (using the Greenhouse-Geisser adjustment and post hoc Newman-Keuls testing). The effect of occlusion was analysed using data from 3-s pre-occlusion until the end of the hidden period. The effect of emergence was analysed using data from 2 s before emergence until 2 s after emergence, with the initial pre-occlusion activity as an additional comparison level.

Identification of recording location

At the completion of each recording track, frontal and lateral X-ray photographs were taken of the monkey's head with the electrode still in place. This enabled the electrode and recorded cells to be localized with respect to specific bone landmarks. In one monkey, during the final recording tracks, electrolytic lesions and dye markers (DiI; Molecular Probes, Europe,) were placed at strategic locations. After transcardial perfusion, the brain was removed from the skull and coronal sections (25 μm) were cut and stained. By aligning the X-ray photographs with the histological sections, cell locations could be determined with an accuracy of about 1 mm. All cells included in this study were located in either the upper or lower bank of STSa, between 12 and 18 mm anterior to the interaural plane. This region includes area STPa (Bruce et al. 1981; areas TPO and PGa: Seltzer and Pandya 1978).

Results

Of 463 cells recorded in STSa, 274 showed visual responsiveness. Of these, 33 (12%) showed significantly elevated levels of activity during the hidden period relative to the pre-occlusion period. Figure 1c shows data averaged across 26 of these neurons each tested with a minimum of 6 s of complete occlusion, from 3-s pre-occlusion until 2 s after emergence. The remaining 7 neurons were recorded for a shorter time period of complete occlusion and are not included in Fig. 1c or in the following population statistical analysis. An ANOVA performed on the population activity in the first 3 periods of the visual stimulus shows a main effect of time ($F_{2.4, 59.8}$=26.5, P<0.00001). There are no significant changes in activity during the pre-occlusion period as the experimenter moves towards the screen (P>0.15, each comparison). The response increases during the occlusion period (when the experimenter is gradually occluded by the screen) compared with pre-occlusion activity (P<0.0004, each comparison) and achieves maximum level after the experimenter has ceased to be visible. Activity slowly decays while the experimenter remains hidden but, even after 6-s post-occlusion, activity is still elevated above the initial pre-occlusion level (P<0.03).

This pattern of activity observed in the population response was consistent across all 33 individual cells. During the first 3 periods of the stimulus, 27 of 33 (82%) neurons tested showed their maximum level of activity when the object was hidden and only the occluding screen was visible. Latency to maximum activity in these 27 cells varied from 1 to 4 s after the onset of the hidden period (e.g. Fig. 2a). Of the remaining 6 cells, 4 showed maximum activity during gradual occlusion (e.g. Fig. 2b) and 2 showed maximum activity immediately prior to occlusion. Duration of the individual cell responses (i.e. activity significantly above pre-occlusion levels) varied from 1 to 11 s after the onset of the hidden period (mean 3.4 s).

Of the 33 cells showing occlusion-related responses to the experimenter, 15 were tested with other three-dimensional objects (e.g. an upright television stand). While this testing was not extensive, form selectivity was suggested in 10 (67%) of these cells, with 9 responding more during occlusion of the experimenter than other objects of similar size moving at the same speed. Conversely, one cell responded more during occlusion of other objects than during occlusion of the experimenter.

Many of the cells (30/33) were tested while the experimenter moved out of sight at different positions within the testing room, varying both in distance from the subject (i.e. near, far) and lateral position (i.e. left, centre and right). Selectivity for the position of occlusion during testing was observed for all 30 cells tested. Most cells (24/30, 80%) showed differential activity according to the lateral position. For example, the responses of the cell represented in Figure 2a were greater following occlusion on the left side of the testing room than in the centre or on the right. One should consider that the direction of movement during both occlusion and emergence also differed between testing on the right and left lateral positions (Fig. 2a, right; conditions a and d).

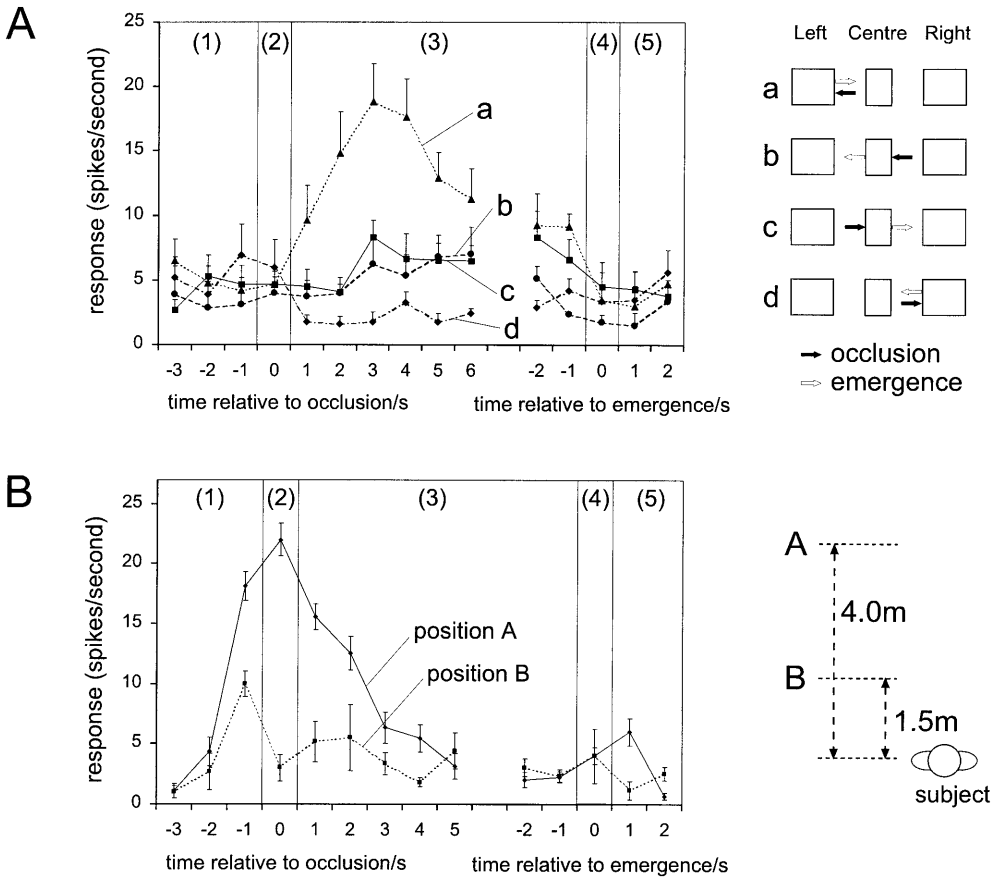

Fig. 2 **a** Responses of a single neuron to occlusion at different lateral positions within the testing room (see *inset on right*). The activity of this neuron was dependent on the position of occlusion within the testing room and not on the direction of movement on occlusion (*solid arrows*) or emergence (*outline arrows*). Two-way repeated-measures ANOVA with time as a within-subjects factor and condition (left; centre, move left; centre, move right; and right: *a–d*, respectively) as a between-subjects factor shows a main effect of both time ($F_{3.5, 97.8}$=4.37, P<0.01) and condition ($F_{3, 28}$=9.24, P<0.005) with a significant time by condition interaction ($F_{10.5, 97.8}$=4.13, P<0.0001). Occlusion on the left elicited significantly greater activity (P<0.05) in the hidden period than all other conditions. Pre-occlusion cell activity did not differ significantly between the conditions (P>0.05). **b** Responses of a single neuron to occlusion at different distances from the subject. The cell gave a large response to occlusion of the experimenter on the subject's left at position *A* (4 m from the subject) and a much smaller response when the occlusion occurred at the same lateral position but at position *B* (1.5 m from the subject). Two-way repeated-measures ANOVA with time as a within-subjects factor and distance as a between-subjects factor shows a main effect of both time ($F_{3.9, 47.0}$=24.7, P<0.00001) and distance ($F_{1, 12}$=51.2, P<0.0001), with a significant time by distance interaction ($F_{3.9, 47.0}$=9.7, P<0.00005). Post hoc testing shows significant difference in activity between the conditions from –1 to +2 s relative to occlusion

For the cell represented in Fig. 2a, however, the lack of response to central occlusion with either movement direction shows that the response during the hidden period was not dependent either on the direction of movement on occlusion or on emergence. Such position selectivity irrespective of the direction of movement was observed in 19 cells.

While these findings indicate that the response of some cells during the hidden period was not explained by the direction of preceding or succeeding motion, this does not exclude an effect of movement direction on specific cells. For example, the response of one cell to an object hidden behind the central screen was present when the object had approached the screen from the left but not from the right. The response of this cell was also modulated by position, with greater responses following occlusion on the right than in the centre.

For 13 of 30 cells (43%), differential activity was observed depending on the distance of testing from the subject. For example, Fig. 2b shows a cell responsive to the experimenter moving out of sight at position a (4 m from the subject). Equivalent testing at position B (1.5 m from the subject) failed to elicit the same changes in activity, particularly in the occlusion and hidden periods. These responses were dependent on the position of occlusion within the room (A vs B) and not on the position of the monkey relative to the occlusion. Moving the position of the monkey relative to the site of occlusion (A) had no effect on response even when the distance between the subject and occlusion was 1.5 m. Such a response profile is characteristic of allocentric rather than egocentric coding, because it does not depend on the observer's vantage-point (Feigenbaum and Rolls 1991).

Positional selectivity was maintained independent of eye position. Cell responses occurred after stimuli were occluded from sight both when the subject fixated the

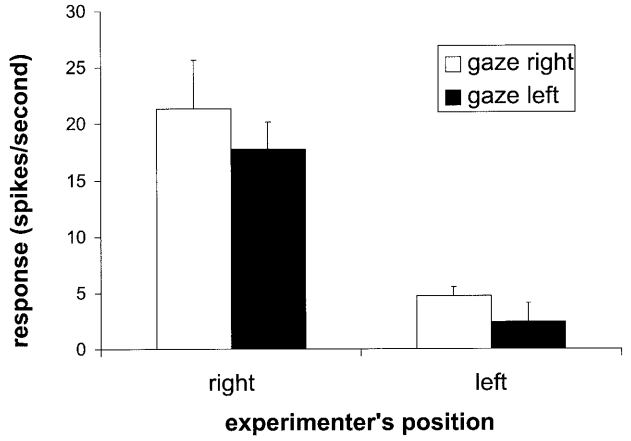

Fig. 3 Spatially selective responses to hidden objects for one cell independent of eye position. For each stimulus condition, 3 trials were selected where eye-gaze was on side of the room for the entire 1-s period directly after occlusion. Overall there was a significantly different response when the experimenter disappeared on the right compared with the left (Mann-Whitney *U*-test, $P<0.004$). Eye position had no significant effect overall on the response (U, $P>0.42$) or on the separate responses to the experimenter disappearing on the right (U, $P>0.37$) or the left (U, $P>0.18$)

occluding screen and fixated elsewhere. Furthermore, fixation of the screen did not produce responses in the absence of a hidden stimulus. Fixation was neither necessary nor sufficient to account for cell responses to hidden stimuli (Fig. 3).

The population of cells we describe was characterised by higher activity during the hidden period than during the pre-occlusion period. Responses related to emergence were less consistent or prominent across individual cells. Of the 26 cells for which data was recorded for at least 2 s after emergence, 15 (57.7%) showed no significant change in activity on emergence, 9 (34.6%) showed increased and 2 (7.7%) showed decreased activity relative to pre-occlusion levels. The magnitude of responses on emergence was not systematically related to the activity during occlusion. At the population level, Figure 1c illustrates that there is a small increase in activity during the gradual emergence of stimuli. This activity during emergence is significantly greater than activity in the 1-s period immediately preceding emergence and activity in the pre-occlusion period ($P<0.04$ each comparison; $F_{2.7, 68.7}=8.5$, $P<0.0001$). After emergence, when stimuli were fully back in view, activity is not significantly different from that prior to occlusion ($P>0.05$).

A small number of cells with the characteristic occlusion response (i.e. increased activity during and following the gradual occlusion of the experimenter) were tested to determine whether the manner of disappearance of the objects was critical in eliciting their response. A large-aperture liquid crystal shutter was placed close to the face of the subject and the experimenter could be removed from view suddenly by closing this shutter. For four of five cells tested with interleaved trials, there was no response to sudden disappearance of the experimenter at the same spatial location as that eliciting a response to gradual occlusion. This suggests that the manner of disappearance may be critical in producing the observed responses and in particular that gradual occlusion may be required.

Discussion

We have described a population of neurons in the banks of STSa that were characterised by large increases in activity following the occlusion of the experimenter (with only the occluder in view) compared with activity prior to occlusion (when the experimenter was moving towards the occluder). Further, such activity was selective for the position of occlusion within the testing room. Provisional testing also suggested that the cells were form-selective, although form selectivity was not rigorously tested, and the apparent selectivity for the experimenter over other objects observed in most of the tested cells could reflect the greater salience of the experimenter. It should be noted, however, that form selectivity is a consistent feature of previously described cell populations within STSa. For the cell population we describe, the prolonged activity during the hidden period appears to arise from the visual event of gradual occlusion rather than from the fact that the objects were not visible.

Since the defining characteristic of the cell population described here is that the greatest activity occurs after an object is completely hidden from view, such cells could contribute to object permanence and be involved in maintaining awareness of the presence and position of predators or conspecifics when they move out of sight.

The spatial sensitivity reported here is consistent with recent accounts (Milner and Goodale 1995; Dijkerman et al. 1998) suggesting that the ventral stream of cortical processing may be required for the allocentric (world-centred) coding of spatial information in contrast to the egocentric coding evident in the dorsal visuo-motor system (Colby 1998). Spatial sensitivity (particularly distance sensitivity) has also been observed in STSa cells responsive to static stimuli (Baker et al. 2000), and both V1 and V4 neurons have been found to be sensitive to the distance of visual stimuli from the subject (V1: Trotter et al. 1996; V4: Dobbins et al. 1998).

An alternative interpretation of the positional selectivity reported here is that it is not spatial *per se* but relates to the emotional significance attached to particular positions within the testing room. It should be noted, however, that different cells were selective for different positions within the testing room (some left, some right, some near, some far) and many different positions were represented. We thus think it unlikely that emotional significance of particular locations within the testing room is responsible for the positional selectivity.

Neurons have been reported previously to respond to stimuli that are no longer in sight. For example, Assad and Maunsell (1995) have reported cells in parietal cortex that maintained directionally selective responses

during the temporary absence of visual stimuli. Cells in premotor cortex (area PMv: Graziano et al. 1997b; or F4/F5: Fogassi et al. 1996) maintain responses to the presence of objects close to the monkey (less than 0.3 m) when the lights are extinguished (Graziano et al. 1997a). A recent report (Umiltà et al. 2001) also shows that neurons in F5 responding to the sight of hand actions (such as grasping an object) continue to respond even if the final part of the action is occluded from sight. In addition, the literature on explicit memory contains many accounts of neurons that are active during the delay period of a memory task (Fuster and Jervey 1982; Miyashita and Chang 1988; Ó Scalaidhe et al. 1997).

The cells presented here differ in important ways from these other reports. First, the neuronal activity in the absence of a visual stimulus has been observed by Assad and Maunsell (1995) in blocks of "inferred motion" trials in which a moving dot briefly disappeared and reappeared at a location consistent with its initial trajectory. This activity was absent in blocks of "blink" trials where the dot blinked off and reappeared at the same location. In individual trials, there was no intrinsic information at the moment of disappearance from which to infer motion or continued existence – there was no occluding screen and no gradual occlusion of stimuli. Thus, on a given trial at the moment of disappearance, continued motion could be inferred only from the blocked nature of the trials. It is not clear how such responses might relate to the capacity for object permanence.

Second, the location of the PMv cells in an area with a high incidence of motor responses suggests that they may be involved in guiding movements to nearby objects in the light or darkness. By contrast, the cells we report, lying in an area associated with visual recognition, appear to provide a perceptually based representation of hidden objects that is not limited to close peri-personal space.

Finally, and most importantly, most other studies reporting activity following the termination of visual stimuli have involved the sudden offset of stimuli and/or performance in explicit memory tasks. Moreover, the activity reported in these studies is generally less than to the objects in view. In contrast we have shown neurons with activity that is much higher following the occlusion of visual objects than prior to occlusion when the objects are fully in view. In terms of visual change, cessation of illumination (Graziano et al. 1997a) and removing a stimulus from a computer display (Miyashita and Chang 1988) lack the gradual occlusion of the object that generates a strong impression of object permanence (Michotte 1950). Such responses are therefore unlikely to contribute directly to such object permanence. In contrast, the evidence reported here suggests that cells in STSa require progressive occlusion of stimuli for prolonged responses in the absence of visual stimuli and are therefore much more likely to be involved in object permanence.

Although the evidence for hidden objects derives from perception, the sustained response we observed goes beyond perceptual experience. The cell activity may thus correspond to an abstract conceptual representation of objects.

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