

Chapter 12

**Responses of single neurons in the  
human brain during flash suppression**

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Number of words: 4616

Number of references: 42

Figures: 6

Keywords: human electrophysiology, single  
cell recordings, medial temporal lobe, flash  
suppression, visual awareness, NCC, neuronal  
correlate of bistable percept

### **12.1. Single neuron recordings in the human brain to explore conscious vision**

Patterns of visual information imaged on the two retinae are transformed into perceptual experiences through multiple hierarchical stages of neuronal processing. A large body of electrophysiological recordings has been concerned with correlating the neuronal responses with the visual input. However, psychophysical investigations have shown that our percepts can be dissociated from the incoming visual signal. The mechanisms of neuronal coding for conscious perception, as well as the whereabouts of the representation of percepts along the visual pathway, remain unclear. Assuming a hierarchical structure for the visual system

(Felleman and Van Essen, 1991), the neuronal responses in early visual areas may reflect the incoming visual input, while the activity in at least some higher parts of cortex should strongly correlate with the subjective, perceptual experience.

We have taken a unique opportunity to record the firing responses of neurons in the human brain and the relation of those responses to perception. Subjects were patients with pharmacologically intractable epilepsy implanted with depth electrodes to localize the seizure onset focus (Fried *et al.*, 1999; Kreiman *et al.*, 2000). The location as well as the number of recording electrodes is based exclusively on clinical criteria. The electrodes are implanted during surgery and cannot be moved by the investigator until they are removed.

Patients stay in the hospital ward, typically for a period of approximately one week<sup>1</sup>.

A schematic representation of the electrodes we use is shown in Figure 12-1A. Through the lumen of the electrodes, eight Pt/Ir microwires were inserted (Fried *et al.*, 1999; Kreiman, 2002). The location of the electrodes was verified by structural magnetic resonance images obtained before removing the electrodes and post-operatively (Figure 12-1B and (Fried *et al.*, 1997; Kreiman *et al.*, 2000)). A sample of the data

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<sup>1</sup>All the experiments described here were conducted in the ward. The studies conformed to the guidelines of the Medical Institutional Review Board at UCLA and were performed with the written consent of the subjects.

thus obtained is shown in Figure 12-1C. Electrophysiological data were amplified, high-pass filtered (with a corner frequency of 300 Hz and digitally stored for off-line processing (Datawave, Denver, Colorado). Individual neurons were discriminated from the extracellular recordings based on the height, width and principal components of the waveforms (Datawave, Denver, Colorado) as shown in Figure 12-1D-E<sup>2</sup>. In those microwires with neuronal recordings (a small fraction of the total as described in (Kreiman, 2002)) we observed an average of 1.72 units per microwire. The information recorded during seizures from the depth electrodes was used to localize the seizure

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<sup>2</sup> Similar results were obtained with a custom, semi-automatic spike sorting algorithm based on a Bayesian approach (Kreiman, 2002).

focus (Ojemann, 1997). While we should note that all the data comes from epileptic patients, more than 80% of the recorded neurons were outside the areas of seizure focus. We did not observe any overall differences when comparing those units within and outside the seizure onset focus in terms of their firing rates, visual selectivity or waveform shape.

We investigated the extent to which the spiking activity from single neurons in the amygdala, hippocampus, entorhinal cortex and parahippocampal gyrus of untrained subjects reflects retinal input versus perceptual experience. We observed that the activity of two-thirds of all visually selective neurons was tightly correlated with the perceptual alternations rather than the retinal input.

## 12.2. Flash suppression phenomenon

Flash suppression constitutes a compelling phenomenon in which the same retinal inputs can give rise to distinct perceptual experiences (Sheinberg and Logothetis, 1997; Wolfe, 1984). It was originally described by Wolfe (Wolfe, 1984) and was inspired by binocular rivalry. Flash suppression entails the perceptual suppression of a monocular image following the sudden onset of a different stimulus to the opposite eye (Figure 12-2). Although two distinct images are presented to the left and right eyes during the 'flash', subjects only see the flashed, novel stimulus. Such a dissociation provides an entry-point for studying the neuronal correlates of visual

consciousness (Blake and Logothetis, 2002; Crick and Koch, 1998; Logothetis, 1998; Myerson *et al.*, 1981). The new stimulus is clearly and consistently observed, suppressing the stimulus previously shown monocularly (Figure 12-2). It is important to emphasize that the same visual input can give rise to very different percepts as can be seen by comparing Figures 12-2A and 12-2B. In this example, during the flash period a photograph of Paul McCartney is shown to the left eye while a grating is presented to the right eye. Yet, depending on which image was already present monocularly, the subject reports seeing only Paul McCartney or only the grating during the flash.

Flash suppression is quite robust to several changes in the stimulation parameters. The monocular presentation time,

$t_{monoc}$ , can vary widely and the effect is very strong for durations above 200 ms. A possible mechanism of suppression would be that the sudden change in stimulation to one eye could bias the competition between the two percepts due to a shift in attentional focus or to a motion/change signal. However, the effect can be observed after introducing a blank interstimulus interval (ISI) between the monocular and flash presentations. The suppression effect remains equally strong for *ISIs* less than 200 ms. A strong disruption (where subjects typically report observing a mixture of the two stimuli) is evident for *ISIs* longer than 500 ms. The flash duration,  $t_{flash}$ , can be as short as 10 ms. A long flash duration produces binocular rivalry (the contralateral stimulus is observed first and then alternation between

the two stimuli takes place). It seems unlikely that the phenomenon can be explained as a form of forward masking or light adaptation since the luminance properties of the monocular stimulus do not affect the suppression and given the invariance of the effect to parameter changes (Kreiman and Koch, 1999; Wolfe, 1984). A recent version of flash suppression shows that the phenomenon can be generalized to elicit suppression in the absence of interocular conflict (Wilke *et al.*, 2002).

Since the onset of perceptual transition is externally controlled, flash suppression allows finer temporal control and collection of more transitions than binocular rivalry, in which fluctuations in perception are spontaneous and, therefore, unpredictable. Given the time constraints of

the clinical environment, we focused on flash suppression. It seems legitimate to question whether the mechanisms of flash suppression coincide with those of binocular rivalry. At a global level, both binocular rivalry and flash suppression involve a competition between two alternative images. In both cases, the same visual input can give rise to two different percepts. One key difference is that the transitions are externally triggered in flash suppression, rather than internally induced as in rivalry. However, it is interesting to note that the minimum duration of  $t_{monoc}$  coincides with the amount of time required to elicit binocular rivalry upon flashing different stimuli to the two eyes (Wolfe, 1984). Furthermore, the neuronal responses in the inferotemporal cortex visual area of the

macaque brain during both phenomena are very similar (Sheinberg and Logothetis, 1997).

### **12.3. Neuronal activity in the human brain during flash suppression**

#### *Neurons that followed the percept*

We recorded the activity of 428 single units in the human medial temporal lobe while subjects reported their percept during flash suppression. The medial temporal lobe (MTL) typically constitutes one of the potential areas suspected to be part of the seizure onset focus. The MTL receives direct input from the inferior temporal cortex, the highest purely visual area (Felleman and Van Essen, 1991; Suzuki, 1996) (Cheng *et al.*, 1997; Saleem and Tanaka, 1996), as well as from olfactory and auditory portions of the

nervous system (Kandel et al., 2000). The MTL plays a prominent role in several explicit memory processes including the storage and retrieval of information (Eichenbaum, 1997; Squire and Zola-Morgan, 1991; Zola-Morgan and Squire, 1993).

Of the 428 MTL neurons, 172 units were in the amygdala, 98 in the hippocampus, 130 in the entorhinal cortex and 28 in the parahippocampal gyrus. The data reported here come from 14 patients (10 right handed, 9 male, 24 to 48 years old).

Images were chosen from natural categories of stimuli and included faces of unknown actors denoting emotional expressions (Ekman, 1976), spatial layouts, famous people, animals and abstract patterns (Kreiman et al., 2000). The two pictures in each flash-suppression trial were

constrained to belong to different categories. Stimuli subtended a visual angle of approximately 3 degrees and were presented separately to the right and left eyes by means of a pair of liquid crystal glasses that transmit light to one or the other eye in interlaced fashion (Crystal Eyes, Stereographics, San Rafael, CA). Subjects were instructed to report their percept by pressing a button to indicate that the original image changed into a different picture or another button if it did not (and by verbal debriefing in 10% of trials). In approximately 10% of the trials, we presented only the monocularly shown image and a blank screen to the other eye during the flash as a control. The monocular stimulus was randomly delivered to either the left or right eye. The suppression

phenomenon is very strong as illustrated by the behavioral results in Figure 12-2C.

The responses of a neuron located in the right amygdala showed a striking pattern of selectivity (Figure 12-3A). This unit showed increased firing rate upon presentation of a black and white drawing of Curly, one of the characters of a well-known American TV comedy. On average, the unit changed its spiking activity from a rate of 1.7 spikes/s during the baseline period to 7.9 spikes/s (two-tailed t test,  $p < 10^{-3}$ ). The neuron did not change its firing rate in response to other faces, or to other black and white drawings (we are not claiming that this is the only possible stimulus to which the neuron would respond -- it simply was the only stimulus in our set of 47 pictures that enhanced its activity.) Other neurons

changed their firing rates in response to more than one stimulus; still other neurons were broadly tuned, enhancing their activity upon presentation of several different pictures from one of the presented categories of stimuli (Kreiman, 2002; Kreiman *et al.*, 2000).

Upon dichoptically presenting the drawing of "Curly" the neuronal response showed a strong dependence on perceptual state. When the picture of Curly was presented monocularly and an ineffective stimulus<sup>3</sup> perceptually suppressed the image of Curly during the flash, the neuron did not enhance its firing above background (Figure 12-3B, left). However, when a different image was presented monocularly and the subject was presented with Curly as

the flashed stimulus, the neuron showed a strong and transient response (Figure 12-3B, right). The response during the flash, in other words, was similar to the response during the monocular presentation only when the subject reported seeing the preferred stimulus.

Figure 12-4 shows a summary of the responses of 12 neurons that responded selectively to one or a few individual images from our stimulus set<sup>4</sup>. These units showed a marked enhancement in firing rate in response to the monocular presentation of the stimulus (Figure 12-4A); they did not respond beyond baseline during the binocular period when the effective stimulus was

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<sup>3</sup> A stimulus that did not cause a change in firing rate in this amygdala cell.

perceptually suppressed (Figure 12-4A) and, finally, they showed a strong enhancement in their firing rate during the dichoptic period when the effective stimulus was consciously perceived (Figure 12-4B).

Approximately 12% (a total of 51 units) of the recorded neurons showed visual selectivity with enough stimulus repetitions during both the monocular presentation and the flash period for analysis<sup>5</sup>. The majority (69%) of these neurons followed the

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<sup>4</sup> The same conclusions apply to 23 other neurons with broad selective responses (see Kreiman *et al.*, 2002 and Figure 12-6A).

<sup>5</sup> As we have reported previously, the majority of recorded neurons did not show visual selectivity. A possible reason for this observation is that many of these units may be non-visual neurons. However, given that we only present a small number of stimuli in a relatively short period of time, it is possible that in many cases we simply fail to find a visual stimulus that drives the cell.

perceptual report of the subjects. In other words, these neurons showed enhanced firing upon presentation of the preferred stimulus during the flash if and only if the image was consciously perceived. We observed neurons that followed the percept in all four areas of the MTL. Given the low number of neurons, it is difficult to draw any conclusion about possible distinctions across regions (the number of neurons that followed the percept ranged from 2 to 18).

The remaining one third of the selective units did not show a statistically significant response during the flash period regardless of the subject's percept (that is, in the presence of the two, conflicting, stimuli). It is unlikely that the lack of response of these neurons is due to the shorter presentation during the flash given

that the latencies of neurons in the MTL seem to be much shorter than  $t_{flash} = 500$  ms (Kreiman *et al.*, 2000). These neurons that did not respond during the flash showed only a weak response during the monocular presentation. It is possible that this weak response was not strong enough to be detected during the flash period. Alternatively, the conflicting presentation of two stimuli perhaps inhibited the response.

Importantly, we did not observe any neuron that responded when the preferred stimulus was not consciously perceived. Even though the preferred stimulus was physically present during the flash period, the neurons in the human medial temporal lobe were oblivious to it unless the subject actually perceived the stimulus.

*Comparison of neuronal responses between  
perception and suppression phases*

We directly compared the responses for those neurons that followed the percept during the two states in which the effective stimuli were subjectively perceived (i.e., when presented monocularly without contralateral stimulation and when presented and seen together with a contralateral stimulus). There was no significant difference in the distribution of the response latencies (Figure 12-4C, two-tailed t test,  $p>0.15$ ), durations (Figure 12-4D,  $p>0.3$ ) or magnitudes evaluated by the total number of spikes (Figure 12-4E,  $p>0.1$ )<sup>6</sup>.

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<sup>6</sup>In contrast, the response to the effective stimulus when it was suppressed and when it was dominant were

Therefore, in spite of the fact that there is a completely different stimulus present on one retina during the dichoptic period, the neuronal responses of these cells are very similar to those when the effective stimulus is presented monocularly. This supports the view that the neurons in the MTL primarily represent the percept rather than the visual input *per se*.

Given that the dichoptic period followed a monocular presentation, it is reasonable to ask whether the absence of response to the suppressed stimulus is a consequence of adaptation of the neuronal response or a lack of response to consecutive presentations of the same preferred stimulus. To address this question we pooled

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virtually independent, with a correlation coefficient

the neuronal responses from all our data set (including previous experiments reported by Kreiman et al., (2000a,b) and re-analyzed all the trials in which the preferred stimulus was presented in two consecutive trials. We did not observe any overall trend indicative of a reduction (nor enhancement) in the neuronal response (Figure 12-5)<sup>7</sup>.

*Correlation between neuronal response and percept*

How strong is the correlation between the single-neuron response and the percept? We

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of just 0.08.

<sup>7</sup>It should be noted that in all these cases, the second presentation occurred at least 1000 ms after the first presentation and there was a behavioral response (button press) in between. In the present experiment, the flash period immediately followed the monocular presentation and there was no response in between these two periods.

analyzed whether it was possible to predict the subject's percept based on the neuronal response. We performed a ROC, signal detection analysis (Green and Swets, 1966) based on the spike counts at the single-trial level. This analysis yields a probability of misclassification of the neuron's preferred stimulus,  $p_e$ , ranging from 0 for perfect prediction to 0.5 for chance levels (since there are two possible choices). Figure 12-6A-B shows how  $p_e$  decreases with increasing time windows used to compute the spike counts. The probability of misclassification during the monocular presentation was very similar to that during the flash period when the preferred stimulus was perceived. In contrast, when the preferred stimulus was perceptually

suppressed, the performance of this classifier was basically at chance levels.

The number of errors of the classifier was quite high for integration windows of less than 200 ms at the level of single neurons. In order to attempt to extrapolate these results to how well small ensembles of neurons could reflect the subject's percept, we trained a Support Vector Machine (Vapnik, 1995) to classify the data into 'perceived' and 'not perceived' categories based on increasingly larger numbers of independent neurons<sup>8</sup>. Figure 12-6C shows how the error

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<sup>8</sup> For this purpose, we estimated the spike density function for each neuron and normalised it to the neuron's peak response (Figure 12-4). The input to the SVM classifier with a linear kernel were the normalized neuronal response integrated over different time windows (Figure 12-6C). The class for each entry was based on the subject's perceptual report. This analysis was restricted to the 23

rate decreased with increasing time windows and number of units. The gain in performance after offset of the flash (500 to 1000 ms after flash onset) is due to the continued response of some neurons beyond the disappearance of the stimuli. It is interesting to observe a slight saturation effect, whereby the increase in performance of the classifier decreases with time, indicating that quite accurate characterization of the percept can be obtained by analyzing 500 ms after flash onset. It should be noted that there are several assumptions here including the independence of neuronal responses. It is conceivable that interactions such as

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broadly tuned neurons due to the very small number of repetitions available for training from the neurons selective to individual stimuli.

synchronous firing could enhance even further the correlation with the percept for small ensembles of neurons.

#### **12.4. In search of the neuronal representation of the percept**

Models describing the perception of bistable images often propose a competition between neuronal populations tuned to one or the other alternative representations of the external world (see chapters 3, 17, 18, this volume). Subjectively, one perceives the end result of this competition with one stimulus predominating over the other except during transition states or piecemeal states. Flash suppression constitutes a particularly

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strong variant where the transition duration is minimal (in most cases too brief to be noticed).

Our results suggest that the spiking activity of most of the visually selective neurons that we recorded from in the medial temporal lobe correlates well, at the single-trial level, with the visual conscious experience of the subject. These results parallel the observations made in the higher stages of the macaque visual system (Sheinberg and Logothetis, 1997). Similar to the data in the monkey inferior temporal cortex, we do not find any evidence for neurons that represent the perceptually suppressed image, that is, the unconscious image, in the MTL.

While our data reflect the end result of the conflict between alternative percepts,

it does not address the issue of where and how the competition is resolved. There is a strong projection from the monkey inferior temporal cortex to the MTL structures in monkeys (Cheng *et al.*, 1997; Logothetis and Sheinberg, 1996; Saleem and Tanaka, 1996; Suzuki, 1996; Tanaka, 1996), however, the detailed neuroanatomy is largely unknown in humans. Functional imaging as well as neurological data suggests a possible involvement of frontal areas during internally driven perceptual transitions (Lumer *et al.*, 1998; Ricci and Blundo, 1990). Single neuron studies in earlier visual areas of the macaque monkey reveal that a progressively higher proportion of neurons correlate with the subjective percept as one ascends the visual hierarchy from the LGN to V1 to V4/MT (Lehky and

Maunsell, 1996; Leopold and Logothetis, 1996; Logothetis and Schall, 1989). For a review see Leopold and Logothetis, 1999). In higher areas, functional imaging also shows a correlation between BOLD measures of activation and perception (Tong *et al*, 1998).

Interestingly, in earlier visual areas, some neurons showed a response that was anti-correlated with the percept. This type of responses was absent in monkey IT cortex as well as in our MTL recordings. Functional imaging shows that activity in V1 may correlate with the percept in binocular rivalry (Polonsky *et al.*, 2000; Tong and Engel, 2001; Tononi *et al.*, 1998). However, as the biophysical basis of the BOLD signal is not yet understood, great care should be exercised in identifying an increase in BOLD

with an increase in firing frequency of neurons (Logothetis *et al.*, 2001).

It has been suggested that overtraining in monkeys may influence the neuronal responses studied during binocular rivalry (Tononi *et al.*, 1998). While it is known that training can modify the pattern of dominance during binocular rivalry (Leopold and Logothetis, 1999), our data show that strong neuronal modulation based on the percept can be found in naïve observers. It is plausible that the neuronal correlate of the percept is transferred from IT to MTL where it might be involved in declarative memory storage processes (Eichenbaum, 1997; Kreiman *et al.*, 2000; Rolls, 2000; Zola-Morgan and Squire, 1993). The proportion of human MTL neurons following the percept is smaller than the values reported for monkey IT cells

(Sheinberg and Logothetis, 1997). These differences could simply be due to the different criteria used to determine neuronal selectivity. They could also be due to differences between species. On the other hand, it is possible that the number of neurons that underlie and generate conscious visual perception peaks in intermediate areas of the brain, such as inferior temporal cortex, and is lower in medial temporal or prefrontal lobe structures (Crick and Koch, 2000; Jackendoff, 1987).

**Figure legends**

**Figure 12-1: Schematic of electrodes, sample of signals and waveforms**

**A.** Schematic of the type of electrodes that were used (Fried *et al.*, 1999; Kreiman, 2002). Wideband activity was monitored 24 hours per day from the Pt-Ir contacts along the electrode for clinical purposes. Single-unit data were acquired through the eight microwires.

**B.** Magnetic resonance image (1.5 Tesla) showing the position of one electrode in the hippocampus.

**C.** Sample extracellular data obtained from one of the microwires after filtering and amplification. The activity of multiple units can be discriminated from the noise in extracellular recordings.

**D.** Spike sorting to isolated individual neurons was performed by separating the clusters in two-dimensional plots of several features of the waveforms. Here we illustrate only a subset of these features that include the first three principal components of the data. Distinct gray tones correspond to different clusters.

**E.** Sample of the waveforms after spike sorting. Each cluster is shown as a separate gray tone.

**Figure 12-2: Flash suppression phenomenon**

**A.** Flash suppression consists of the perceptual suppression of an image that was previously shown monocularly upon flashing a new stimulus to the contralateral eye. The left panel shows the stimulus presentation while the right panel depicts the subjective

perceptual report. In this example, a photograph of Paul McCartney is shown monocularly for 1000 ms after which a horizontal grating is flashed onto the opposite eye for 500 ms, while, the same picture is shown to the original eye. Subjects were instructed to report their percept in a two-alternative forced-choice manner after the disappearance of the flash.

**B.** Flash suppression test depicting the complementary condition to that in **A**. During the flash period, the stimuli presented to the two eyes are the same as in **A**. However, the subjective percept is exactly the opposite.

**C.** Percentage of suppression based on the 2AFC report (black bars) or upon debriefing (gray bars) for the flash suppression trials (FS) and the control trials (C).

**Figure 12-3: Sample of neuronal response**

**A.** Visual selectivity of a neuron in the right amygdala. Raster plots and post-stimulus time histograms (aligned to stimulus onset) of the neuronal responses to a subsample of 12 pictures (out of 47 presented pictures; (Kreiman, 2002)). The neuron enhanced its firing rate only upon presentation of the face of the comedian Curly, shown within a gray-shaded box. The horizontal dashed line shows the overall mean firing rate of this unit (1.7 Hz). Some of the stimuli were in color but are shown here in black and white. The number of presentations is indicated in the upper left corner of the histograms. Bin size = 200 ms.

**B.** Responses of the neuron during the flash-suppression test to the image of Curly. The

format is the same as in panel **A**. On the left, the neuronal responses were aligned to the onset of the monocular presentation of Curly (indicated by the first vertical dashed line). An ineffective stimulus was flashed (at the time indicated by the second vertical dashed line) and perceptually suppressed the image of Curly. On the right, an ineffective stimulus was shown monocularly. The image of Curly was flashed and perceptually suppressed the ineffective stimulus.

**Figure 12-4 Summary of neuronal responses**

**A-B.** Average normalized spike-density function obtained by convolving the spike train with a fixed gaussian of 200 ms and dividing by the peak activity (n = 12 neurons selective to individual stimuli). **A.**

The dark gray trace corresponds to the responses aligned to the time of presentation of the monocular preferred stimulus; the light gray corresponds to the responses to all other stimuli. **B.** The dark gray traces correspond to the responses aligned to the onset of the flash of the preferred stimulus after a different stimulus had been presented monocularly; the light gray trace identifies all other presentations. The shaded regions correspond to 95% confidence intervals. The vertical dashed lines denote the monocular and flash onset respectively.

**C.** Distribution of response latencies during the monocular (top) and flash (bottom) presentations (n=35 neurons). Bin size = 50 ms. **D.** Distribution of response durations during the monocular and flash

presentations. Bin size = 50 ms. **E.**

Distribution of the magnitude of the response during the monocular and flash presentations. Bin size = 2 spikes/s.

**Figure 12-5. Lack of change in response to consecutive presentation of the preferred stimuli.**

Distribution of the change in firing rate for consecutive presentations of preferred stimuli. For this figure, we pooled data from several different experiments (Kreiman et al., 2002; Kreiman et al., 2000a,b) (n = 104 neurons). The main plot shows the ratio of firing rate in one presentation to that in the previous presentation (mean ratio =  $1.23 \pm 1.55$ , median ratio = 0.94). Bin size = 0.1 (only points with non-null firing rates

were included here). The inset shows the difference in firing rates (all points included here, mean difference =  $-0.07 \pm 4.84$  spikes/s). Bin size = 1 spike/s.

**Figure 12-6 Estimating the percept from the neuronal response**

ROC analysis showing the probability of misclassifying the subject's perceptual report ( $p_e$ ,  $0 \leq p_e \leq 0.5$ ) based on the spike counts in different time windows. **(A)** 23 neurons broadly tuned to categories of natural stimuli. **(B)** 12 neurons selective to individual images. The time window starts 100 ms after stimulus or flash onset (circles: monocular stimulus; squares/triangles: perceived/suppressed flash period respectively). **(C)**

Classification of the subject's perceptual report using a linear SVM (Vapnik, 1995) after pooling different numbers of broadly tuned, independently firing neurons. We used the implementation of SVM classifiers by Rifkin (Rifkin, 2000) with the following parameters: linear cost per unit violation of the margin = 2, tolerance for the Karush-Kuhn-Tucker conditions =  $10^{-4}$  (see Vapnik, 1995), equal weights for false alarms and miss errors, linear kernel with normalizer = 1. The x-axis denotes the time from onset of the flash. In all cases, the data were split evenly and randomly between training and test sets (we tested leave-one-out cross-validation in a random subset of 20% of the cases and this yielded similar results). The normalized spike density function of each neuron was computed by convolving the spike

train with a fixed width gaussian of 100 ms and dividing by the peak response. The normalized neuronal responses during the flash period of 1, 2, 5 or 10 neurons integrated over the indicated time windows were used as input to a SVM classifier with a linear kernel to discriminate between those trials in which subjects reported perceiving the preferred stimulus or the non-preferred stimulus. The size of the marker indicates the number of neurons. For  $n = 1$ , we averaged over 20 possible selections of neurons. For  $n = 2, 5$  and  $10$ , we averaged over 50 random combinations of  $n$  neurons. As discussed in the text, it should be noted that there are many strong assumptions underlying this computation, including that the firing rates of these neurons are independent.

We would like to thank Geraint Rees, Nikos Logothetis and John Allman for advice throughout this work, all patients for their participation, Ryan Rifkin for support with the SVM analysis and Eve Isham, Charles Wilson, Tony Fields and Eric Behnke for help with the recordings. This work was supported by grants from NIMH, NINDS, NSF, the Mettler Fund for Research Relating to Autism, the McDonnell-Pew Program in Cognitive Neuroscience, the W.M. Keck Foundation Fund for Discovery in Basic Medical Research and a Whiteman Fellowship to GK. Parts of this report were described previously (Kreiman, 2002; Kreiman *et al.*, 2002).

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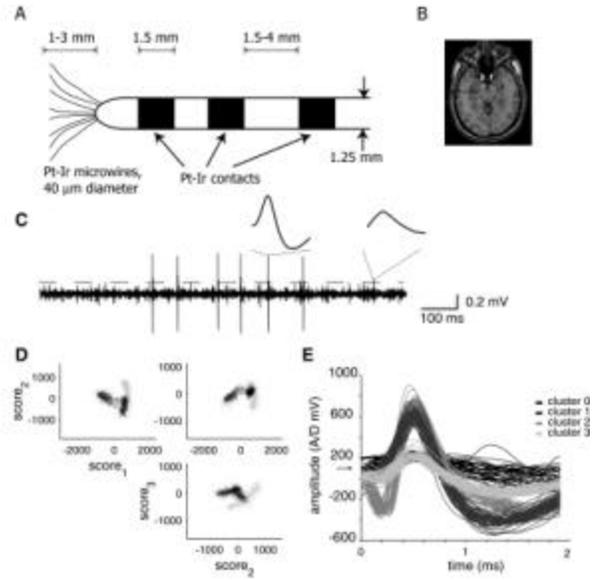
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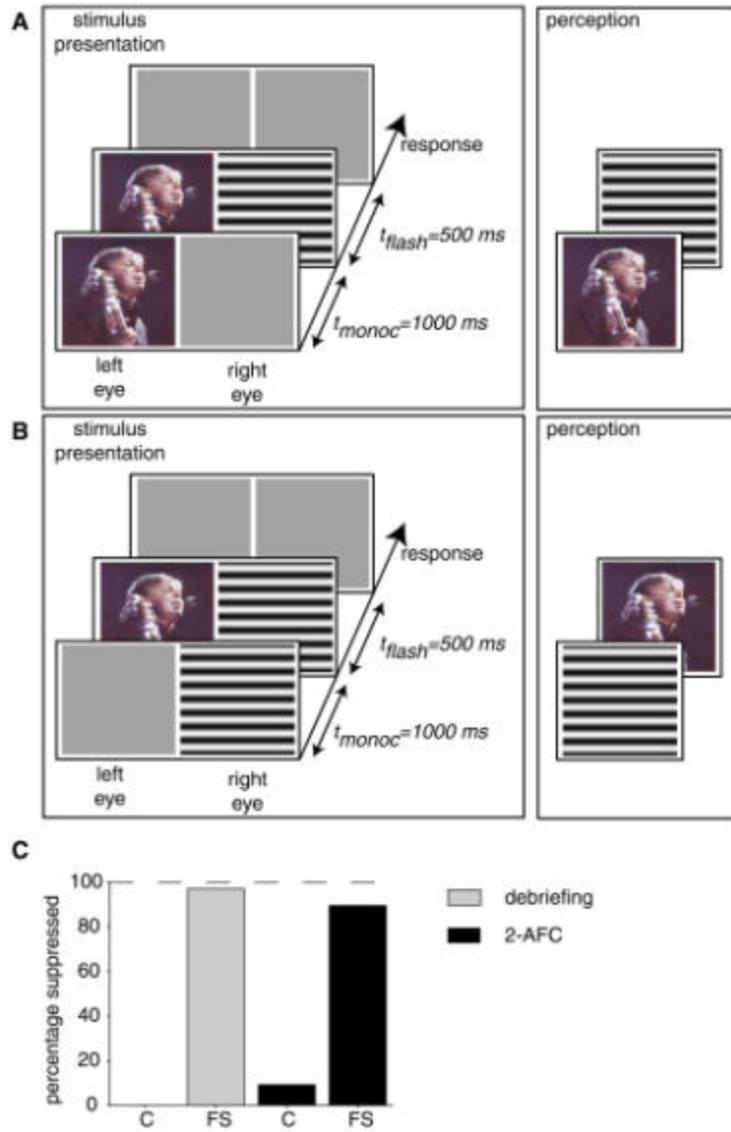
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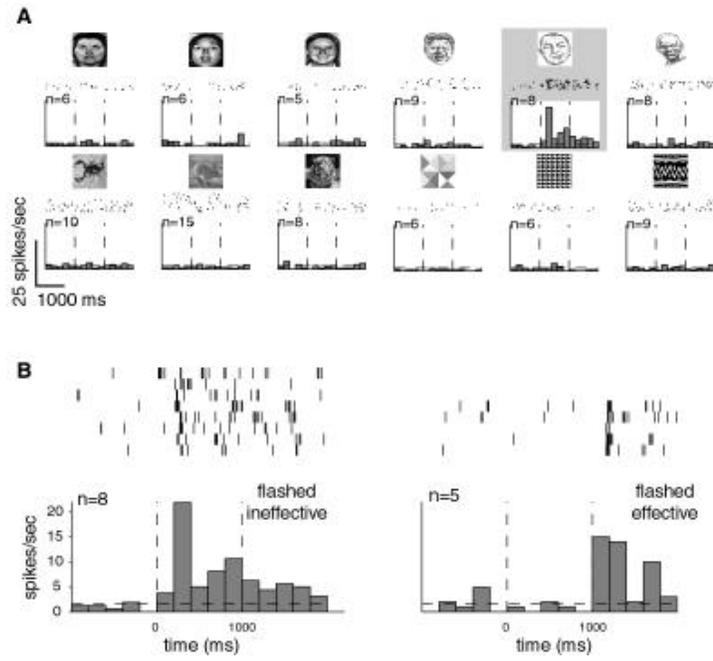
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Neuronal responses during flash suppression in the human brain  
Figure 12-1



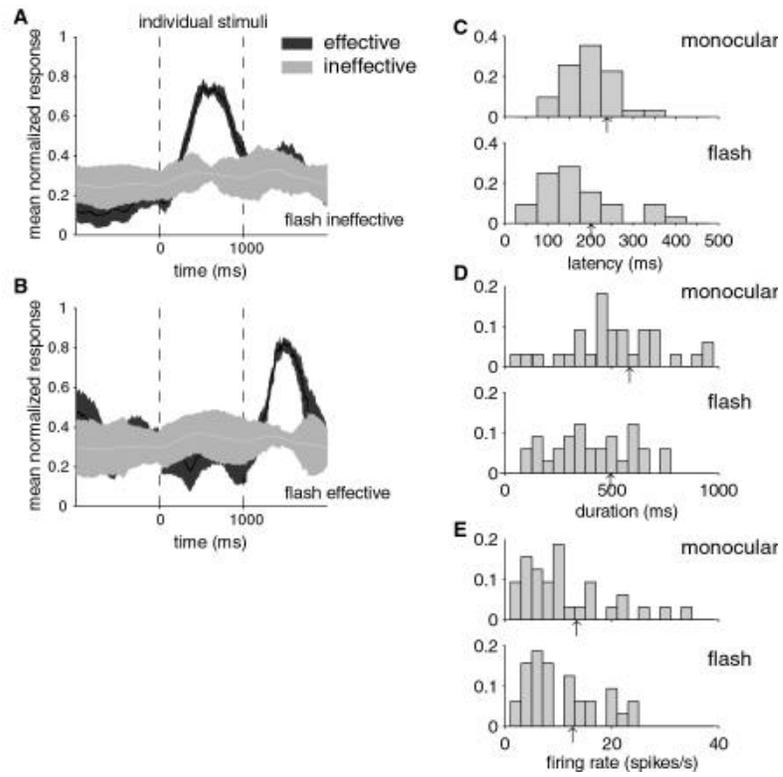
Kreiman *et al.*  
Neuronal responses during flash suppression in the human brain  
Figure 12-2



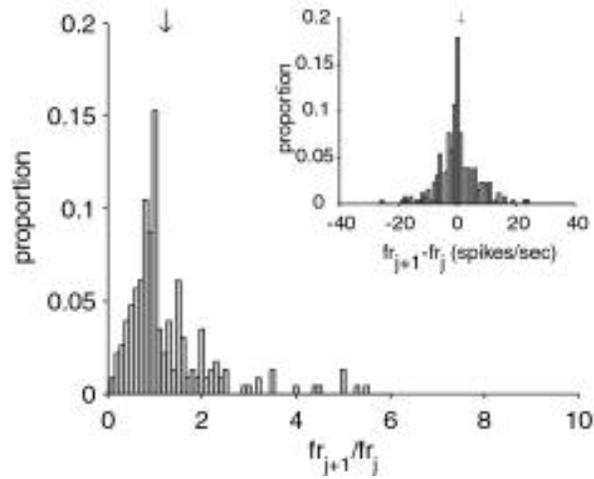
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Neuronal responses during flash suppression in the human brain  
Figure 12-3



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Neuronal responses during flash suppression in the human brain  
Figure 12-4



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Neuronal responses during flash suppression in the human brain  
Figure 12-5



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Neuronal activity during flash suppression in humans

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Neuronal responses during flash suppression in the human brain  
Figure 12-6

