Single-neuron correlates of subjective vision in the human medial temporal lobe

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Visual information from the environment is transformed into perceptual sensations through several stages of neuronal processing. Flash suppression constitutes a striking example in which the same retinal input can give rise to two different conscious visual percepts. We directly recorded the responses of individual neurons during flash suppression in the human amygdala, entorhinal cortex, hippocampus, and parahippocampal gyrus, allowing us to explore the neuronal responses in untrained subjects at a high spatial and temporal resolution in the medial temporal lobe. Subjects were patients with pharmacologically intractable epilepsy implanted with depth electrodes to localize the seizure onset focus. We observed that the activity of two thirds of all visually selective neurons followed the perceptual alternations rather than the retinal input. None of the selective neurons responded to a perceptually suppressed stimulus. Therefore, the activity of most individual neurons in the medial temporal lobe of naive human subjects directly correlates with the phenomenal visual experience.

In bistable visual illusions, as in the Necker cube, the same retinal input can be associated with two very different subjective percepts (1, 2). Such dissociations provide an entry point for studying the neuronal correlates of visual consciousness (3). Although the neuronal responses in early visual areas will reflect the incoming visual input, the activity in at least some higher cortical areas should strongly correlate with the subjects' percept. *Flash suppression* constitutes a striking example in which the same input can give rise to two distinct percepts (4–6). It consists of the perceptual suppression of a monocular stimulus upon flashing a different stimulus to the contralateral eye while keeping the original stimulus in the ipsilateral eye (Fig. 1). Although two distinct stimuli are presented to the left and right eyes, subjects only "see" the flashed, novel stimulus. We investigated the extent to which spiking activity from single neurons in the human medial temporal lobe (MTL) reflects retinal input or phenomenal percept. We find that the majority of the neurons follow the subjective percept.

Materials and Methods

Subjects. Subjects were 14 patients (10 right-handed, 9 male, 24–48 years old) with pharmacologically intractable epilepsy implanted with depth electrodes to localize the focus of seizure onset. The targets were based exclusively on clinical criteria. All studies conformed to the guidelines of the Medical Institutional Review Board at the University of California (Los Angeles) and were performed with the written consent of the subjects.

Recordings. We report here the activity for all probes within the entorhinal cortex, hippocampus, amygdala, and parahippocampal gyrus. Through the lumen of the electrodes eight Pt/Ir microwires were inserted (7–10). The location of the electrodes was verified by structural magnetic resonance and computer tomography images obtained before removing the electrodes (8, 9). Electrophysiological data were amplified, high-pass-filtered (>300 Hz), and stored digitally for off-line processing (Datawave, Denver). Individual neurons were discriminated from the extracellular recordings based on the height, width, and principal components of the waveforms (Datawave). We obtained an average of 1.72 units per microwire. The information recorded during seizures from the depth electrodes was used to localize the seizure focus (11). We did not observe any statistically significant difference between the neurons within and outside the seizure focus in terms of firing rates, visual selectivity, or waveform shape. Eighty percent of the neurons and 89% of the visually selective units were outside the seizure focus; therefore, our results would be unaltered if we were to exclude the neurons within the seizure focus from the analysis.

Stimulus and Behavioral Responses. A stimulus was presented monocularly, and immediately afterward the same stimulus was flashed onto the same eye while a different stimulus was flashed onto the contralateral eye (Fig. 1). The two pictures in each flash-suppression trial were constrained to belong to different categories and could not include two human faces. Other than these constraints, the pictures as well as the order from trial to trial were chosen pseudorandomly. The stimuli subtended a visual angle of $\approx 3^\circ$ 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). The duration of the monocular presentation was 1,000 ms (1,500 ms in two subjects), and the duration of the binocular period was 500 ms (300 ms in five subjects). There was no intervening blank interval between the monocular presentation and the flashed images. Both images disappeared after the flash, which indicated the subject to give his/her response. Subjects were asked to report by pressing two buttons whether the original image changed into a different picture or not. In $\approx 10\%$ of the trials, only the monocular image was presented in the ipsilateral eye during the flash as a control. The monocular stimulus was delivered randomly to either the left or right eye. The total number of presentations depended on clinical constraints and ranged from 116 to 510. We only analyzed the responses to stimuli if we had a minimum of four presentations per image during each test. Perceptual suppression is very strong (4, 5, 7, 12). The average percentage of suppression was $94 \pm 3\%$. We also verified this perceptual suppression by debriefing the subjects, asking them to describe what they had seen in 20% of the trials. Suppression was observed in more than 96% of the trials from the debriefing reports. The few trials in which subjects significantly moved or in which they made a mistake in the response were discarded from analysis. We did not monitor the eye movements. In a brief control experiment, seven patients were asked to make a saccade to one of four locations indicated by a cross. We did not observe any neurons that responded to eye movements and visual stimuli similarly to what has been reported in electrophysiological recordings in the temporal lobe in monkeys.

Abbreviation: MTL, medial temporal lobe.

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Data Analysis. The criteria and methods for data analysis were described previously (7, 8). Briefly, visual selectivity was analyzed during the monocular presentation (using the interval [100;1,000) ms with respect to stimulus onset) and compared across stimuli, across categories, and to the baseline (using the interval [−1,000;0) ms with respect to stimulus onset). A neuron was considered to be visually selective if its response was statistically different from the baseline and from that to the other stimuli. Both parametric (ANOVA and *t* test) and nonparametric (bootstrapping) tests were used to evaluate the statistical significance of the results (the values shown in the text correspond to the parametric results, but there were no major differences between the two). Selectivity was analyzed also during the binocular period (using either the interval [100;600) or [100;1,000) ms after flash onset; results using both intervals were similar and we report here only those using the first interval). A unit was considered to "follow the percept" of a particular stimulus *A* (or a particular category *A*) if (*i*) its response during the monocular presentation was *selective* to *A* as defined above, (*ii*) its response during the binocular period when *A* had been presented monocularly and a different stimulus was flashed onto the contralateral eye was indistinguishable from baseline, and (*iii*) its response during the binocular period was selective to *A* when another stimulus had been presented monocularly. The spike density function (Fig. 4) was obtained by convolving the spike train with a 200-ms width Gaussian. The latency and duration were computed by estimating the time at which the response departed from baseline by more than 2 standard deviations. Finally, the receiver operating characteristic analysis was performed as described (7, 8) by comparing the responses after presenting the preferred and nonpreferred stimuli.

Results

We recorded the activity of 428 single units in the human MTL while the subjects reported their subjective percept in a flash-suppression paradigm (Fig. 1 and Table 1). A stimulus was presented monocularly (a picture of former president Clinton in this example) during 1,000 ms. Immediately after this, the same stimulus was flashed onto the same ipsilateral eye while a different stimulus (an abstract pattern in this case) was flashed onto the contralateral eye for 500 ms (Fig. 1*a Left*). During the binocular period, the new stimulus perceptually suppressed the picture in the other eye (Fig. 1*b Left*). In the reverse experiment, the picture of Clinton suppressed the pattern that had been shown monocularly (Fig. 1 *a* and *b*, *Right*). Subjects were patients with intractable epilepsy implanted with depth electrodes for localizing the seizure onset focus for potential clinical resection (7–9). Based on clinical criteria, electrode probes were placed in MTL targets bilaterally (Table 1), which permitted us to record in a stable manner from individual neurons while patients performed the test reporting their percept. Images were chosen from natural categories of stimuli and included faces of unknown actors denoting emotional expressions (Ekman faces), houses and spatial layouts, photographs and drawings of famous people, photographs of animals, and abstract patterns (7, 8).

Neuronal Responses During Flash Suppression. An exemplary response of a right amygdala neuron in one subject is shown in Fig. 1. The cell's firing rate increased from a baseline of 2.8 to an average of 15.1 spikes per sec after monocularly presenting an image of Clinton. The neuron failed to respond to any of 49 other pictures (two-tailed *t* test comparison against baseline and against the other stimuli, $P < 0.01$; Fig. 1 *c* and *f*, *Left*; see *Materials and Methods*). The neuron responded selectively to three different images of Clinton. Here we only show the responses to two of those pictures; for the third one we could obtain only two repetitions during the binocular period. When Clinton was presented binocularly after a different image was shown monocularly, subjects indicated that they saw Clinton, and the neuron responded by increasing its rate to 9.2 spikes per sec (two-tailed *t* test comparison against baseline and against the other stimuli, $P < 0.01$; Fig. 1 *c* and *f*, *Right*). Yet the neuron did not react when a picture of Clinton was presented during the flash but was perceptually suppressed by stimuli ineffective in driving this neuron (a black and white pattern in Fig. 1*c Left* and a horizontal grating in Fig. 1*f Left*; two-tailed *t* test comparison against baseline, $P > 0.1$). Note that the picture of Clinton appeared in the input during the binocular period in both cases, yet the percept and the neuronal response were completely different (compare Fig. 1*b Left* versus *Right* and 1*e Left* versus *Right*).

The activity of another amygdala neuron is illustrated in Fig. 2. This cell enhanced its firing rate for some but not all faces. Because the responses to the selected faces were indistinguishable statistically (ANOVA, $P > 0.1$), the data were merged. The neuron increased its rate upon monocular presentation of these effective stimuli but not when the preferred stimuli were flashed but perceptually suppressed by ineffective stimuli (Fig. 2*a*). When the effective stimuli were flashed and perceptually dominant, the neuron increased its firing response (Fig. 2*b*).

We previously reported that some MTL cells responded to different pictures belonging to the same category of stimuli (7, 8). The response of one of these neurons located in the parahippocampal gyrus is summarized in Fig. 3. It increased its firing rate upon presentation of pictures of spatial layouts and not to other groups of stimuli (there was no significant difference in the comparison of the responses to distinct individual stimuli within the spatial layouts category; one-way ANOVA, $P > 0.1$). The neuron fired more vigorously when the effective stimuli were presented monocularly, and its activity was indistinguishable from baseline when the effective stimuli were perceptually suppressed (Fig. 3*a*). When the effective stimuli were flashed and became dominant after a different stimulus was presented monocularly, the neuron enhanced its firing rate (Fig. 3*b*). There was no change in the firing rate over baseline for any other group of stimuli.

Comparison of Neuronal Response Between Perception and Suppression Phases. Our observations for the population of neurons that we studied are summarized in Table 1 and Fig. 4. Of 428 MTL neurons, 44 (10.3%) showed a selective response to a category and 32 (7.5%) to individual stimuli. Note that these are distinct populations of neurons (see *Materials and Methods*). Of those, only 33 and 18 neurons, respectively, had enough data collected during flash suppression for further analysis. The 33 category-selective neurons (such as the example shown in Fig. 3) showed selectivity during monocular presentation. Twenty-three of them (70%) were selective also during the binocular period when the preferred stimulus was perceptually dominant. Of the 18 neurons that responded selectively to individual stimuli (such as the examples shown in Figs. 1 and 2), 12 neurons (67%) were selective also during the flash when the preferred stimulus was perceptually dominant. None of the total of 51 visually selective neurons showed any enhanced response to the preferred stimulus when it was physically present on the retina but perceptually suppressed.

The average normalized responses of the neurons that followed the percept reveal three aspects (Fig. 4). First, these units show a marked increase in their response to the monocular presentation of their effective stimulus. Second, they do not respond beyond baseline during the binocular period when the effective stimulus is perceptually suppressed by an ineffective stimulus. Finally, they show a strong enhancement in their firing rate during the binocular period when the effective stimulus is perceived consciously by the patients, which is true for both

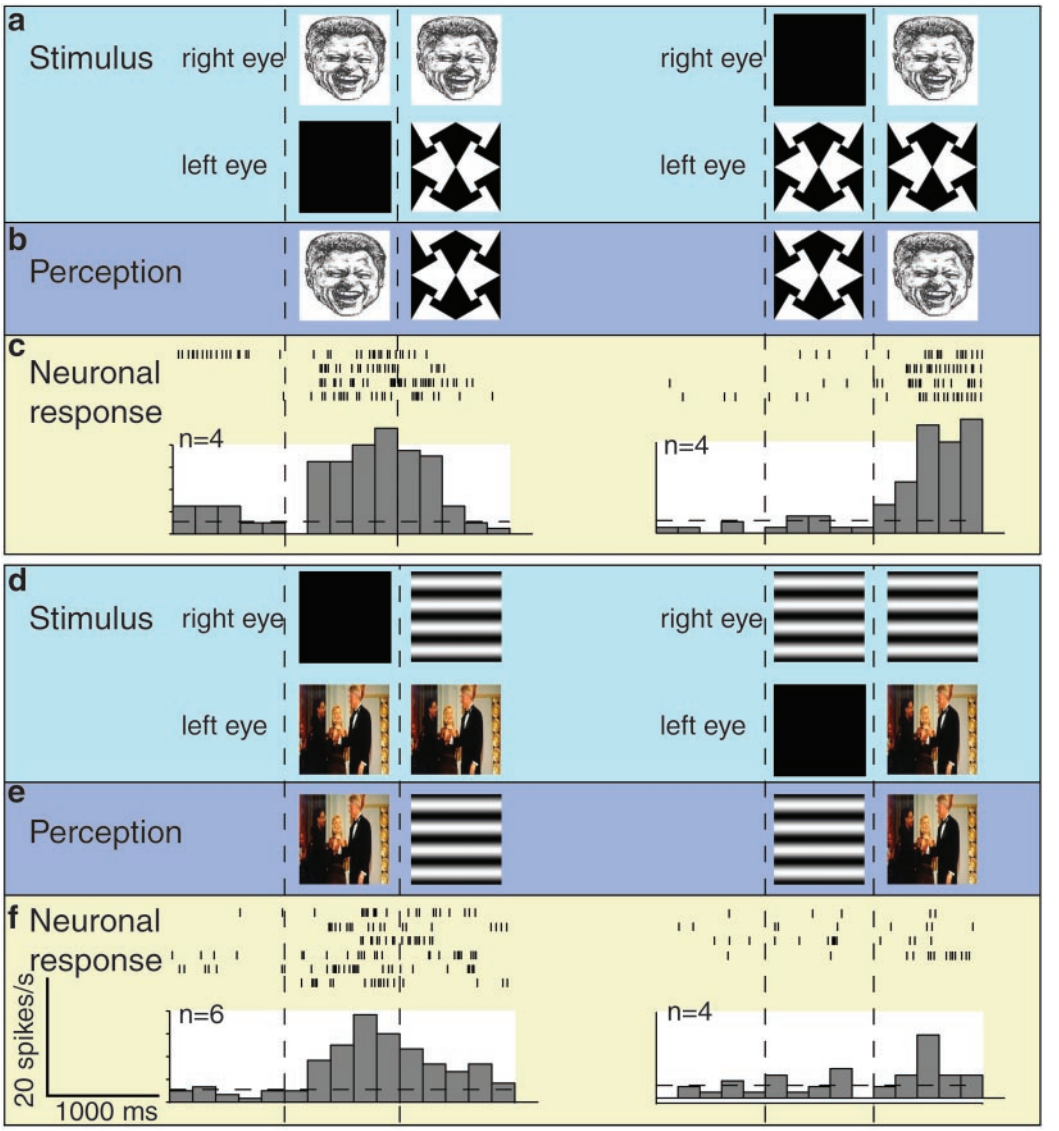

Fig. 1. Right amygdala neuron that follows the subjective percept. (*a*) Stimulus presentation: an image is presented monocularly for 1,000 ms. The same image then is flashed onto the same ipsilateral eye while a different image is flashed to the contralateral eye for 500 ms. (*Left*) A picture of Clinton is presented monocularly, and a black and white pattern is later flashed onto the other eye. (*Right*) The pattern is presented monocularly, and Clinton is flashed to the contralateral eye. Images were chosen randomly with the constraint that the two pictures could not belong to the same category. (*b*) Subjective percept. (*Left*) The picture of Clinton is suppressed during the binocular period by the pattern. (*Right*) The picture of Clinton perceptually suppresses the pattern. (*c*) This neuron responded selectively to Clinton among 49 different stimuli (see *Materials and Methods*). (*Left*) Responses when Clinton was shown monocularly and a different ineffective stimulus was flashed. Although there seems to be elevated firing activity during the binocular period, it is not statistically significant after taking into account the response latency. (*Right*) Responses when an ineffective stimulus was shown monocularly and the picture of Clinton was flashed and perceptually suppressed the ineffective stimulus. Bin size, 200 ms. The dashed lines denote the onset of the monocular image and the flash. The horizontal dashed line shows the baseline activity of the neuron (2.8 Hz). The number of repetitions of each stimulus is shown above the histogram. (*d–f*) Responses of the same neuron to a different image of Clinton. The unit also responded selectively to a third picture that depicted a photograph of Clinton. However, we did not have a sufficient number of presentations of that picture during the binocular period ($n = 2$); therefore, we are not showing those responses here (7).

category- (Fig. 4 *a* and *c*) and individual-selective (Fig. 4 *b* and *d*) neurons. Approximately one third of the selective neurons did not follow the percept (Table 1); they responded selectively during the monocular presentation, and they did not fire when their effective stimulus was present but perceptually suppressed, yet they failed to enhance their activity during the binocular period even in those cases when the effective stimulus was perceived. It is possible that the lack of response of these neurons is caused by the shorter presentation during the flash. This explanation seems unlikely given that the latencies of neurons in the MTL seem to be much shorter than the 500 ms of the flash presentation (8) and that we have observed strong responses during the binocular period in other neurons (e.g., Figs. 1–3). Another possibility is that the response of these neurons was inhibited somehow by the presence of another stimulus in the other eye. A third possibility is that the lack of response during the binocular period was simply caused by a weaker response that is sufficient to reach significance during the monocular presentation but not during the binocular period. The activity of the selective cells that did not follow the percept was weaker as evidenced by the P values that in most cases were between 0.01 and 0.05, whereas the P values of most (78%) of the selective neurons that did follow the percept were below 0.01.

We directly compared the responses for those neurons that

Table 1. Total number of units and number of selective units tested in each location

	Amy	Hipp	EC	PHG	Total
n	172	98	130	28	428
Category selective	15	10	4	4	33
Number that followed percept	11	8	2	2	23 (70%)
Image selective	10	4	1	3	18
Number that followed percept	7	3	0	2	12 (67%)

n is the total number of units recorded in each location (Amy, amygdala; Hipp, hippocampus; EC, entorhinal cortex; PHG, parahippocampal gyrus). Data from the right and left hemispheres were merged. ''Category selective'' indicates the units that were category-selective during the monocular presentation and were tested during the flash presentation with a sufficient number of repetitions and stimuli (see *Materials and Methods*). There were seven additional category-selective units that could not be tested during the binocular period. Of the 33 selective units, ''number that followed percept'' indicates those neurons that followed the percept. Similarly, ''Image selective'' denotes the units that showed selectivity to individual stimuli, and ''number that followed percept'' indicates the neurons that followed the percept (12 additional selective units could not be tested during the binocular period).

followed the percept during the two states in which the effective stimuli were perceived subjectively: the monocular presentation and the flashed period when both the effective and ineffective stimuli were present. There was no significant difference in the distribution of the response latencies (two-tailed t test, $P > 0.15$), response durations ($P > 0.3$), or the response magnitude evaluated by the firing rate ($P > 0.1$). Therefore, despite the fact that there is a completely different stimulus present on one retina during the binocular period, the neuronal responses of these cells are very similar to those when the effective stimulus is presented monocularly. In contrast, the correlation coefficient between the response to the flash of the effective stimulus when it was perceived and when it was suppressed was 0.08, and the two distributions were significantly different (two-tailed t test, $P < 10^{-4}$). Note that the effective stimulus is present in both cases, and yet the neuronal activity is strikingly different (Figs. 1–3).

Correlation Between Neuronal Response and Percept. How strong is the correlation between the single-neuron response and the percept? We addressed this question quantitatively by performing a receiver operating characteristic analysis (8, 13). We computed the probability of misclassification, p_e, in predicting the subject's percept of the effective stimulus based on the firing rate for those neurons that followed the percept (p_e ranges from 0 for perfect classification to 0.5 for chance performance). There was a strong correlation between p_e during monocular presentations and the binocular period when the effective stimuli were perceived (Fig. 5 *a* and *b*). The values of p_e during either period were clearly lower (indicating a better performance) than those obtained during the binocular period when the effective stimulus was suppressed from perception (gray area in Fig. 5 *a* and *b*, $P < 10^{-4}$ for category-selective neurons and $P < 10^{-5}$ for neurons selective to individual stimuli). Indeed, when the preferred stimulus of the neuron was not perceived, the probability of misclassification was statistically indistinguishable from chance levels ($P > 0.2$ gray area in Fig. 5 *a* and *b*).

Discussion

Flash suppression is not a complicated version of forward masking and cannot be explained by light adaptation or other mechanisms that reduce the visibility of the ipsilateral flash (4, 12). A short blank offset can be introduced between the monocular presentation and the flash without changing the effect. The suppression is not caused by the offset reversing the dominance of the eyes, because it can be elicited in the absence of any offsets.

It is not clear how flash suppression relates to another bistable phenomenon, binocular rivalry (1, 4, 5, 12, 14). The neuronal basis of binocular rivalry has been investigated intensely both at the single-cell level in trained monkeys (5, 14–16) as well as by using magnetoencephalography and functional brain imaging in humans (17–21).

In our subjects, two of every three selective MTL neurons modulate their activity with the percept (Table 1). Furthermore, their firing rate was not elevated to stimuli that were present physically but perceptually suppressed. In other words, we did not find any evidence for a neuronal representation of perceptually suppressed images in the MTL.

Our results parallel observations in the higher visual stages of the macaque (5). Sheinberg and Logothetis found that the fraction of neurons coding for the percept during flash suppression reached 90% of all selective neurons in inferior temporal cortex and the superior temporal sulcus. In monkeys, there is a strong connection between the inferior temporal cortex and the MTL structures from which we recorded (22, 23).

It is important to note that monkeys are highly overtrained in the binocular rivalry and flash-suppression tasks (5, 21). Train-

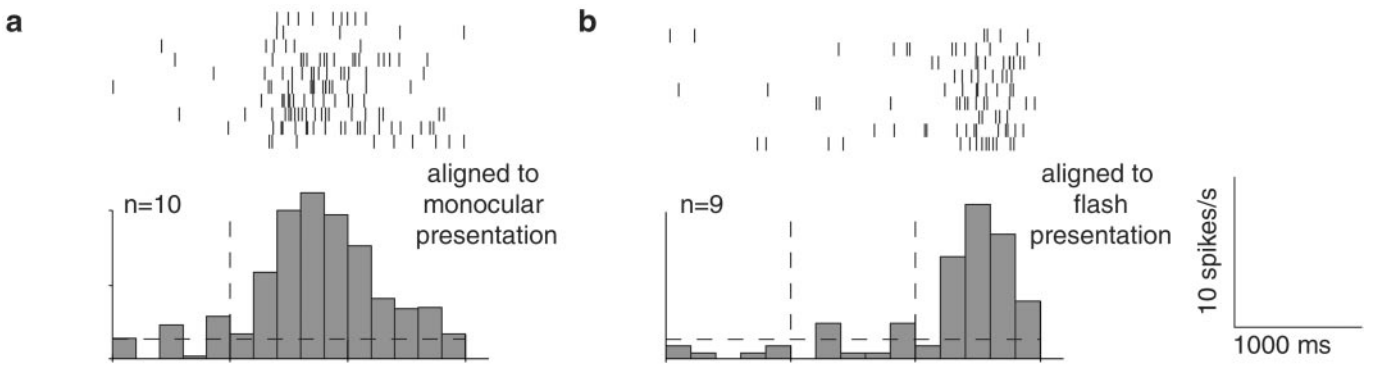

Fig. 2. Another neuron that follows the percept. Responses of a neuron in the right amygdala (in a different subject from the one in Fig. 1) that showed a selective response to four different faces from a set of 42 different stimuli. For two of those stimuli, we did not have a sufficient number of presentations during the binocular period. We therefore show the average response only to the other two stimuli (a photograph of Paul McCartney and one of the Ekman faces). (*a*) Responses in those cases where the effective stimuli were shown monocularly and perceptually suppressed during the flash by an ineffective stimulus. (*b*) Responses during those trials in which an ineffective stimulus was shown monocularly and the effective stimuli were flashed. The cell responded if and only if the effective stimulus was perceived subjectively.

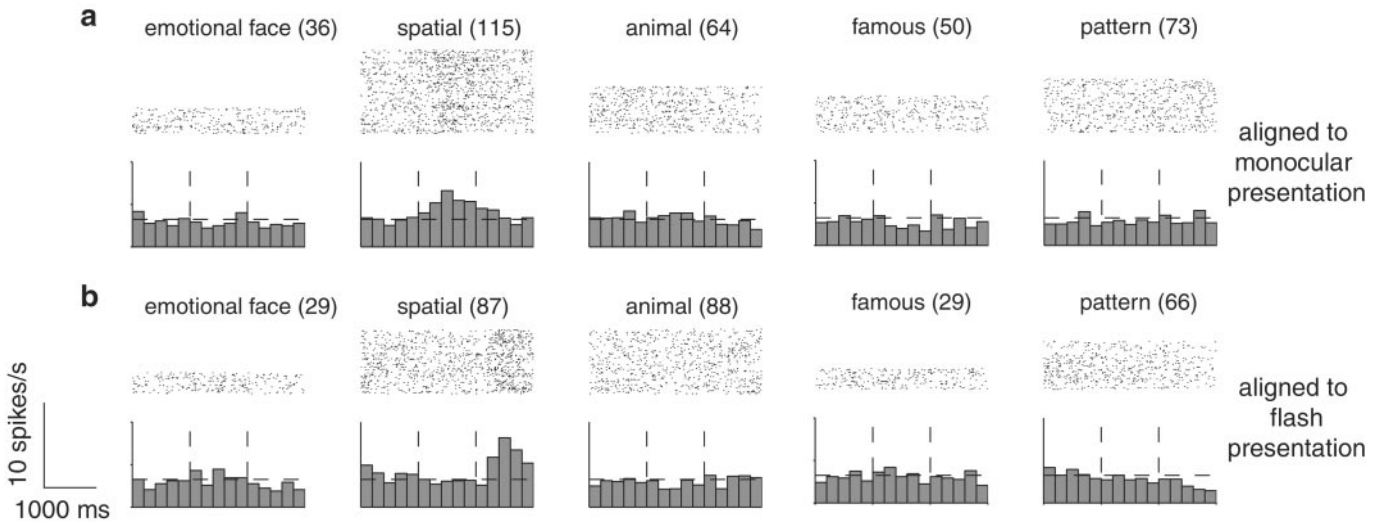

Fig. 3. Responses of a category-selective neuron located in the parahippocampal gyrus of a different patient. The neuron responded selectively to spatial layouts. (*a*) Responses averaged for all the trials in which a stimulus from the indicated category was presented monocularly and a stimulus from a different category was flashed during the binocular period. (*b*) Responses averaged over those trials in which stimuli from the indicated category were flashed during the binocular period after stimuli from a different category were presented monocularly. The neuron only enhanced its firing rate during those intervals in which the effective stimuli were perceived and not when they were suppressed. Although there was variability from one picture to another within the spatial layouts, there was no significant difference in the ANOVA comparing the across-picture variability to the variability after repeated presentations of the same picture ($P >$ 0.1 during monocular and $P > 0.2$ during binocular presentation).

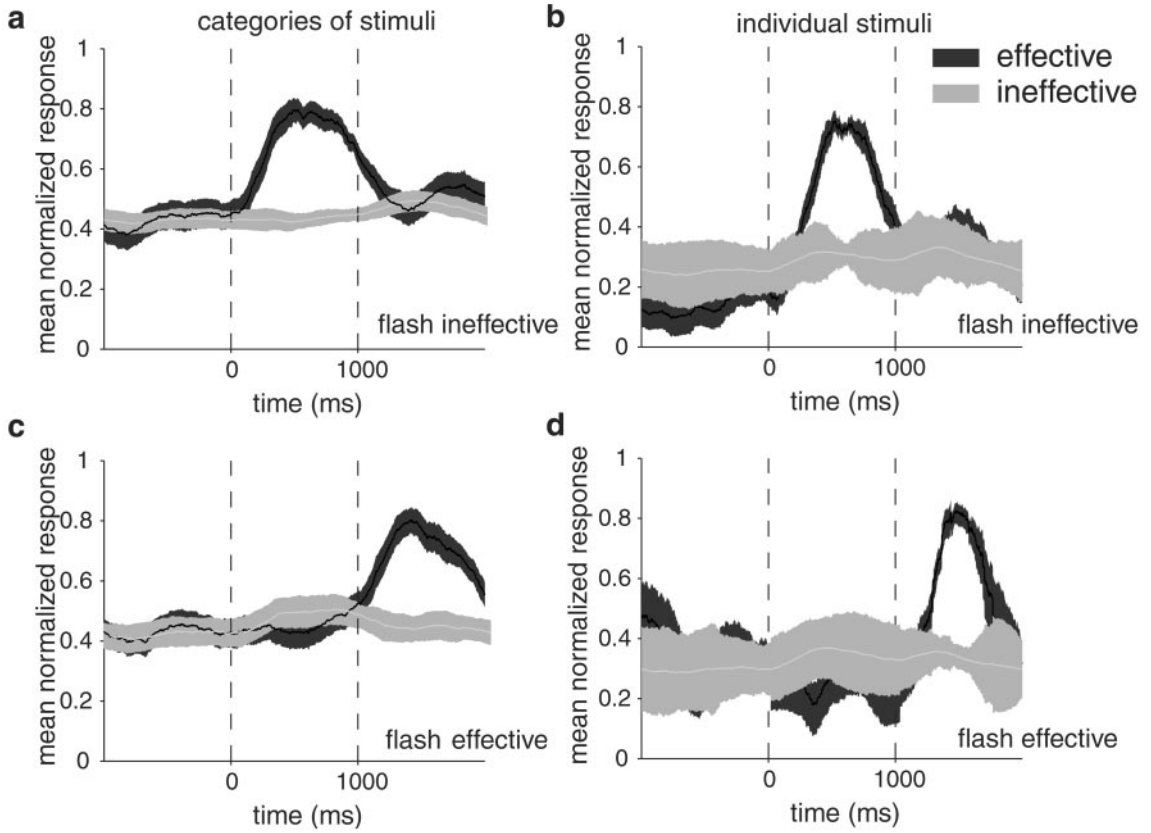

Fig. 4. Average normalized spike density function removed this. (*a–d*) Mean normalized spike density function to effective and ineffective stimuli (obtained by convolving the spike train with a 200-ms width Gaussian and normalizing by the peak activity). Only those neurons that followed the percept were averaged in the plot. The average was computed separately for those units that were category-selective (*a* and *c*) and those that were image-selective (*b* and *d*). The dark gray trace in *a* and *b* shows the average activity for those trials when the effective stimulus was shown monocularly and an ineffective stimulus was flashed. The light gray trace shows the average response to all the other stimuli. The shaded regions correspond to 95% confidence intervals. The vertical dashed lines denote the time of monocular presentation and flash onset, respectively. The dark gray trace in *c* and *d* shows the average activity for those trials in which an ineffective stimulus was shown monocularly and the effective stimuli were dominant during the binocular period. The light gray trace shows the average response to all other stimuli.

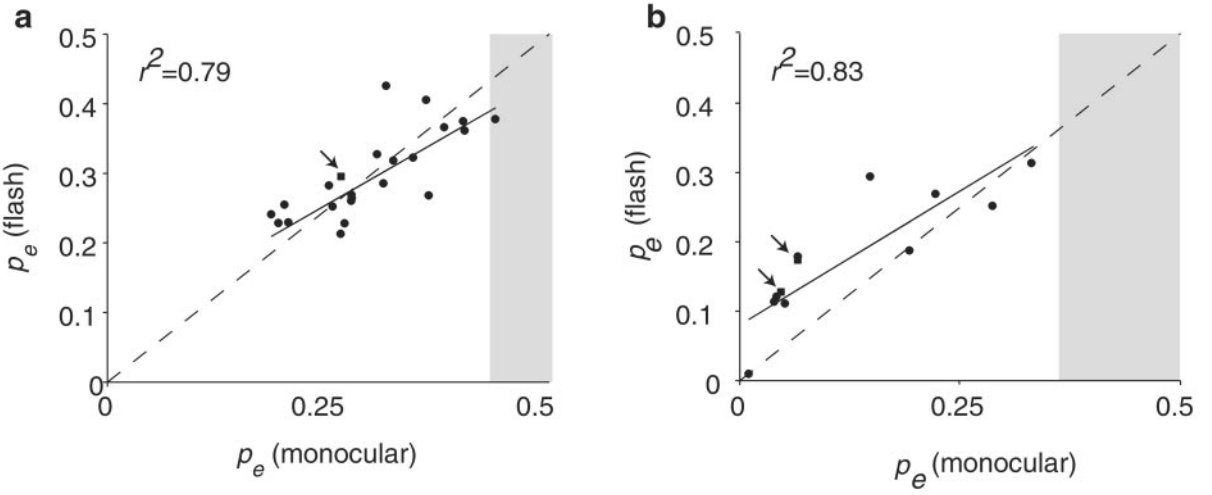

Fig. 5. Probability of misclassification (p_e) in predicting the presence of the effective stimulus for each cell during the monocular or flash presentation period based on the firing rate. Direct comparison of p_e during the monocular presentation and the binocular period when the effective stimulus is perceived for category-selective units (*a*) and neurons selective to individual stimuli (*b*). The dashed diagonal shows the $y = x$ line. The solid line corresponds to the linear fit ($r^2 = 0.79$ and 0.83, respectively). The arrows show the examples from the previous figures. The shaded rectangles show the 95% confidence intervals for the p_e values for the preferred stimuli when they were presented during the flash but were perceptually suppressed. These values were statistically indistinguishable from chance levels.

ing can affect dominance changes during binocular rivalry (14). It is unclear to what extent this overtraining can alter the neuronal responses, but there is evidence that practicing and training can alter tuning curves in earlier visual areas (24). Some investigators have suggested that the responses obtained in monkeys could be caused by the effects of training rather than the perceptual changes *per se* (21). Our results provide evidence to the contrary by showing that strong neuronal responses that follow the subjective percept can be found in naive human observers.

It is plausible that the neuronal correlate of the percept is transferred from the inferior temporal to the MTL where it might be involved in declarative memory storage processes (25–28). The proportion of human MTL neurons following the percept is smaller than the values reported for monkey inferotemporal cells (5). These differences could simply be caused by the different criteria used to determine neuronal selectivity; they also could be caused by differences between species. On the other hand, it is possible that the number of neurons that underlie conscious visual perception peaks in intermediate areas of the brain such as inferior temporal cortex and is lower in MTL or prefrontal lobe structures (29, 30).

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