Discrete place fields of hippocampal formation interneurons

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ABSTRACT

The spike discharge of hippocampal excitatory principal cells, also called ‘place cells’, is highly location-specific, but the discharge of local inhibitory interneurons is thought to display relatively low spatial specificity. Whereas in other brain regions, such as sensory neocortex, the activity of interneurons is often exquisitely stimulus selective and directly determines the responses of neighboring excitatory neurons, the activity of hippocampal interneurons typically lacks the requisite specificity needed to shape the defined structure of principal cell fields. Here we show that hippocampal formation interneurons have ‘ON’ fields (abrupt increases in activity) and ‘OFF’ fields (abrupt decreases in activity) that are associated with the same location-specific informational content, spatial resolution, and dependence on context as the ‘place fields’ of CA1 principal cells. This establishes that interneurons have well defined place fields, which has important implications for understanding how the hippocampus represents spatial information.
INTRODUCTION

Defining the local network mechanisms responsible for the response properties of neurons is critical to understanding brain function. In 1971 O’Keefe and Dostrovsky demonstrated that hippocampal pyramidal neurons exhibit peaks in activity, also known as ‘place fields’, that are highly specific to particular regions of an environment (O’Keefe and Dostrovsky 1971). Subsequent to this landmark finding, a large body of experimental work has detailed the spatially-specific activity patterns of excitatory neurons in the CA1, CA3, and dentate gyrus (DG) sub-regions of the hippocampus (Eichenbaum et al. 1990; Ferbinteanu and Shapiro 2003; Knierim et al. 1995; McNaughton et al. 1983; O’Keefe and Conway 1978; Wilson and McNaughton 1993; Wood and Dudchenko 2003). From such work it can be concluded that the spatial firing fields of excitatory neurons, also known as ‘principal’ neurons, arise from a complex interaction between the spatial arrangement of environment cues and self-motion information. The exact spatiotemporal dynamics of the excitatory and inhibitory synaptic inputs underlying the spatially discrete output of principal cells are unknown, but insight into the contribution of the local network inhibitory synaptic inputs can be garnered via an in depth analysis of the spatial activity patterns of local interneurons.

The extent to which hippocampal interneurons are predisposed to exhibit fine-scale spatial firing fields is unknown. In behaving rats, the activity of some CA1 GABAergic neurons (hereafter referred to as ‘interneurons’) is reliably spatially modulated (Ego-Stengel and Wilson 2007; Frank et al. 2001; Kubie et al. 1990; Marshall et al. 2002; McNaughton et al. 1983). However, they are often reported to exhibit broad
firing fields and are not thought of as ‘place cells’ per se. As a result, interneurons reportedly exhibit much less spatial specificity than principal neurons (Frank et al. 2001), and their firing rate is more considered for its relationship to other variables such as network oscillations (Csicsvari et al. 1999; O'Keefe 1976; Ranck 1973) and speed of movement (McNaughton et al. 1983). Taken together, there is a lack of consensus regarding the degree to which interneurons exhibit spatially specific activity, and it is unknown to what extent their activity could shape the spatial activity patterns of excitatory (or ‘place’) cells.

The characterization of interneuron spatial firing fields in previous work may have been hampered by the fact that the metrics designed to quantify or identify ‘place fields’ were optimized based on principal neuron firing patterns. These commonly used metrics may not be objective when applied to interneurons which exhibit much higher mean firing rates and are active, to some degree, over nearly the full extent of a given environment. Consequently, the picture put forth by previous experiments may not have provided a uniformly accurate depiction of interneuron spatial activity patterns.

To overcome such issues, we employed a recently developed measure referred to as ‘positional information’ (Olypher et al. 2003) to directly compare the spatial firing patterns of principal cells and interneurons from the subiculum, CA1, and dentate gyrus. This measure computes relative entropy, which is the distinction (sometimes termed the ‘distance’) between two probability distributions (Cover and Thomas, 2006). In this case, the ‘distance’ computed is that between the probability distribution of firing rates for a given location and the distribution of firing rates across all locations. From the perspective of an ideal observer, this analysis yields a positional information value for
each position within the environment that essentially reflects the degree to which knowledge of the firing rate at any given time is increased by knowledge of the animal’s position in space. High values for positional information are obtained when the average firing rate for a given location is both unique to that location and associated with minimal variability. As demonstrated by Olypher et al. (2003), the measurement of positional information captures the attributes of an ideal ‘place cell’ which fires reliably at one location and is relatively silent everywhere else.

In the present work, we determined whether interneurons were capable of providing a similar degree of positional information. Because interneuron firing fields have previously been described as spatially broad (relative to principal neuron place fields), we also tested whether interneuron firing fields were similar in size to those of principal neurons. In addition, we compared the speed in which (i.e., how abruptly) peak in-field firing rates were reached, relative to baseline firing rates, for interneurons and principal cells. Finally, the directional dependence of interneuron firing fields was examined because principal neuron ‘place fields’ on a track-like environment are often dependent on the animal’s direction of travel (McNaughton et al., 1983).

Interneurons in all three regions exhibited robust, spatially-specific ‘ON’ and ‘OFF’ firing fields that were comparable in width, positional information, abruptness of rate change, and directional dependence to the classic ‘place fields’ of hippocampal principal cells. Of the interneurons for which the animal’s running speed did not contribute to variability in firing rate, over 75% had one or more discrete fields. These findings suggest that a large subpopulation of interneurons provide a discrete inhibitory and/or disinhibitory output. Thus, it would seem reasonable to hypothesize that inhibition
and disinhibition shape the place-specific firing fields of principal neurons in the subiculum, CA1, and DG.

MATERIALS AND METHODS

Behavioral Training

8 adult male Sprague-Dawley rats were trained to run back and forth between two reward locations on a track style maze. The distance traveled between the reward locations was 232 cm, and the width of the maze at any given spot was 12 cm. Initially, rats received a piece of a Cheerio at both reward locations regardless of the route the rat chose to get to the reward location. Eventually the rats were trained to run to the reward location via a specific path after the center intersection or they would not receive a reward at the reward location. The path segment to use was indicated by an interchangeable textured portion of the wall near the beginning of the traversal. To summarize, the rats began a traversal, encountered the path indicator, freely chose straight or left at the first intersection without contingency of reward, arrived at the center intersection, chose one of the two paths that would get them to the reward location, and then received a reward at the goal location only if they chose the path segment that corresponded with the indicator at the start of the traversal. The indicator was randomly interchanged throughout a session with at least 8 changes per day. Training took place over 2-4 weeks and by the end of training all animals would traverse to the reward location via the correct path segment greater than 80% of the time. The maze was in a dimly-lit room surrounded by a black curtain.
Surgery

After behavioral training, the animals were implanted with custom-fabricated microdrives containing 24 stereotrodes. Animals were anesthetized with isoflurane and placed on a stereotaxic table. The skull was cleaned, etched, and dried, and then approximately 7-9 anchor screws were inserted into the skull. Bilateral craniotomies were then made and the underlying dura mater was excised. The electrodes were inserted 0.5-1.0 mm deep in the brain over their respective targets and the exposed brain was covered in Neuroseal (Neuronexus Technologies, Ann Arbor, MI). Dental cement was used to fix the microdrives to the skull and support screws. Rats were allowed to recover for 6 days after surgery during which time feeding was ad libitum. The target coordinates relative to bregma were 2.9 mm lateral and 6.10 mm posterior for the subiculum and 4.0 mm lateral and 5.30 mm posterior for CA1 and dentate gyrus. There were 4 stereotrode bundles, each with 5-7 stereotrodes, placed in cortex above each target.

Electrophysiology

Stereotrodes were constructed by twisting pairs of 25 µm, polyimide-insulated, tungsten wire (California Fine Wire, Grover Beach, CA) and lightly heating with a heat gun. The wires were gold-plated to a final impedance of approximately 100 kΩ. The drives were fabricated from a combination of screws, cannulas, and fun plastic. The stereotrodes were lowered between 0.08 to 0.32 mm each day. The majority of recordings were made prior to moving the electrodes on any given day.

During recording sessions, the microdrive was connected to a custom made head stage (NBLabs, Denison, TX) that used field effect transistors for current amplification,
and red emitting LEDs for behavioral tracking. Signals were relayed to amplifiers (Neuralynx, Tucson, AZ) and then computers running AD acquisition software (Matt Wilson and Loren Frank). The signals were filtered between 600 and 6 KHz, digitized at 32 KHz, and amplified by 5000 -30,000. A video camera and tracking system (DragonTracker, Boulder, CO) was used to record the position of the rat, via the LEDs on the head stage, with a sampling rate of 60Hz and spatial resolution of 5 mm/pixel. Custom-made software (Matt Wilson) was used to discriminate individual units based on waveform parameters from the records on each electrode of a stereotrode pair. The discrimination method has been described in detail before (Kargo and Nitz 2003; Nitz and McNaughton 2004).

Histology

Animals were perfused under deep anesthesia with a formalin solution and the brains were removed for dissection. The brains were sliced in 50 µm sections and Nissl stained. The mediolateral dispersion of each track was obvious as was the final depth. The anatomical depth was then compared to the recorded microdrive depth to ensure that the two were in register. In addition, the anatomical evidence and microdrive records were corroborated by EEG signals such as sharp-wave ripple events, theta oscillations, and gamma oscillations.

Delineating putative interneurons and putative principal cells

Cells were categorized as being either putatively excitatory or inhibitory based on spike width and firing rate (Fig. 1). This method has been employed for extracellular
recordings from different brain regions including the hippocampus (Fox and Ranck 1981; Frank et al. 2001; Simons 1978). The spike width was taken from the electrode of the stereotrode pair with the largest amplitude spike. The extracellular record is, in theory, the first derivative of the intracellular record of the action potential. In practice, the extracellular spike is a slightly slower approximation of the first derivative, but the width of the action potential can be accurately determined by distinct points on the extracellular record and interneurons and pyramidal cells can be delineated by this measure (Henze et al. 2000). In the extracellular record, there is an obvious spike onset representing the initiation of the action potential, a negative peak representing the upstroke of the action potential, and a positive peak representing the peak rate of the rapid hyperpolarizing phase of the action potential. The spike width reported here is from the onset of the extracellular spike record to the positive peak. This is thought to represent the full action potential width (Henze et al. 2000). Our values ranged from 0.24 - 0.42 ms, which is a relatively short duration intracellular action potential, but this only indicates that the extracellular record may better represent the first derivative of the action potential. That being the case, the values reported here may better reflect the half-width of the action potential and the width of interneuron spikes should be less than 0.32 ms. This is a rather conservative cutoff and limits the potential misclassification of excitatory cells. In addition, putative GABAergic fast spiking units in the subiculum are clearly delineated from other classes of cells by a very brief spike width (Anderson and O'Mara 2003). Thus, it is unlikely that any of the identified subicular putative interneurons were falsely classified. Since interneurons are known to have higher firing rates and excitatory neurons lower firing rates, all interneurons (Fig 1, gray box at left) had to have an
average firing rate greater than 15 Hz and all excitatory cells less than 15 Hz (Fig. 1, grey box at bottom right). Since interneurons are also known to have a characteristic theta modulation and lack a prominent complex-spike burst, interneurons that lacked evidence of theta modulation or displayed a prominent burst were eliminated (N=3).

Statistics and Analyses

There is no strict uniform set of criteria used for determining the existence or size of spatial firing fields. Somewhat recently, researchers have begun to use information theoretic analyses and other related analyses to quantify the spatial activity of hippocampal cells. The most commonly used analysis is given by the formula (Skaggs et al. 1993):

\[
I_{\text{spike}} = \sum_i P\left(\frac{\lambda_i}{\lambda}\right) \log_2 \left(\frac{\lambda_i}{\lambda}\right)
\]

\(I_{\text{spike}}\) = information, measured in bits, per spike

\(i\) = position index

\(\lambda_i\) = firing rate at that position

\(\lambda\) = mean firing rate over all positions

In this formula there is an obvious inverse relationship between the information value and mean firing rate, and thus the formula is optimized to yield high values for classic CA1 "place cells" that exhibit high discharge rate at one position, but are relatively silent everywhere else.

More recently, however, it has been shown that other analyses may be better suited to investigate the location-specific informational content provided by individual cells. Here we use one such measure, that of ‘positional information’, described by
Olypher et al. (2003). The determination of positional information is a specific application of the formula for ‘relative entropy’ as described by Cover and Thomas (2006). As applied in this work, relative entropy (i.e., positional information) reflects the inefficiency in assuming that the distribution of firing rates across all 100 ms time periods (thus all locations) is the same as that for all 100 ms time periods associated with a particular location. Specifically, the measure computes the distinction between two probability distributions which are: 1) the probability of observing a given spike count across all 100 ms time windows (thus all locations) ; and 2) the probability of observing a given spike count across all 100 ms time windows associated with a particular location. The distinction between the two probability distributions is determined separately for each location in the environment. The resulting ‘positional information’ value (or, $I_{pos}(x_i)$) essentially reflects the degree to which knowledge of firing rate is increased by knowledge of the animal’s location (Olypher et al., 2003). The mean value $I_{pos}(x_i)$ across all locations is equal to the mutual information, $I(X;K)$ between the position and spike count variables (Olypher et al., 2003).

For all cells, the amount of positional information for each specific location, $I_{pos}(x_i)$, and the mutual information between position and spike count, $I(X;K)$, was calculated (Olypher et al. 2003;).

$$I_{pos}(x_i) = \sum P(k \mid x_i) \log_2 \left( \frac{P(k \mid x_i)}{P(k)} \right)$$

$P(k) = \text{Probability of observing response } k$

$P(k \mid x_i) = \text{Probability of observing response } k \text{ at position } x_i$

For both probability distributions, responses (k) are the number of spikes in a 100 ms time window. For a given direction, responses and the position ($x_i$) of the animal at
the time of each response were recorded for the duration of all trials. Positions \( (x_i) \) had a spatial resolution of 5 cm in the direction of travel of the rat by the width of the track, which was 12 cm. Only trials in which the animal traversed from the start to goal without stopping for more than 4 s at any given spot or reversing direction were used. For a position to be included in the analysis the rat had to encounter that position on at least 8 trials.

The maximum positional information value possible depends upon both the number of possible positions that the animal can take and the number of different spike counts possible. In the present experiments, the highest possible \( I_{\text{pos}}(x_i) \) value is 6.29 bits. This would be the value obtained for a single position if a cell discharged spikes at just that position and nowhere else. Note, however, that in this case, \( I(X;K) \) would then only be 0.10 because \( I_{\text{pos}}(x_i) \) would be 0.02 bits at all other locations. Across all positions the most informative cell would reliably fire at a different rate at each position thereby producing a high degree of \( I_{\text{pos}}(x_i) \) at each position and a high value of \( I(X;K) \).

Directionality was calculated using the formula:

\[
\text{Directionality} = \frac{(rate_{\text{IN}} - rate_{\text{mean}}) - (rate_{\text{OUT}} - rate_{\text{mean}})}{(rate_{\text{IN}} - rate_{\text{mean}}) + (rate_{\text{OUT}} - rate_{\text{mean}})}
\]

Finally, to determine if a cell’s firing rate was dependent on movement velocity, firing rate versus movement velocity was plotted and a least squares-analysis was performed. Given that the number of observations (45) is the same for all neurons examined for a given traversal, \( r \) values less than 0.33 are associated with \( P \) values >0.05 and are thus considered not statistically significant. Therefore, coefficient of determination \( (r^2) \) values of less than 0.10 a priori indicate that movement velocity did not significantly contribute to the variation in firing rate.
RESULTS

Database and task

From 8 animals, recordings of 475 neurons were obtained that were verified anatomically to reside within the hippocampal formation (subiculum: n=264, CA1: n=92, dentate gyrus: n=119). Using the duration of the extracellular spike waveform and the average firing rate (Fox and Ranck 1981; Frank et al. 2001; Simons 1978), 93% of the neurons were categorized as being either a putative principal cell (Fig. 1; n= 383) or a putative interneuron (Fig. 1; n=59). See methods for more information.

In this navigational task, rats were allowed to freely traverse from a start location to a goal location via 4 different partially overlapping routes. Reward at the goal location was dependent on the particular path segments chosen (see methods). A textured indicator near the start of the traversal indicated which path segment to take, and the indicator was randomly switched throughout a recording session.

CA1 spatial firing fields

To form the basis for quantitative comparison, the fields of classically identified CA1 ‘place cells’ were defined using a recently developed analysis (Olypher et al. 2003). Opposed to a commonly used information theoretic analysis used in the field (Gothard et al. 1996; Hargreaves et al. 2005; Nitz and McNaughton 1999; Skaggs et al. 1993), this metric quantifies the informational content of the spike discharge of a cell at each specific location within an environment. Firing rate data from two representative CA1 cells are shown (Fig. 2).
First, a conservative determination of the existence of a firing field was made based on the firing rate. This ensures that the quantification of a spatial firing field was based on data from neurons that would have been identified as ‘place cells’ by essentially any criterion. A field existed if a cell’s firing rate exceeded 4 times its baseline rate at a given position, exceeded a minimum average rate of 4 Hz at that position, and was at least twice its baseline rate for two consecutive 5 cm positions. Spatial maps of the average firing rate across all trials when the animal ran IN (left) or OUT (right) are shown for Cell 1 (Fig. 2A, top). Cell 1 had one field traveling IN as well as one field traveling OUT (Fig. 2A).

The informational content provided by the spike discharge of the cell was quantified. Two measures were calculated: the amount of positional information provided for each specific position ($I_{\text{pos}}(x_i)$), and the mean positional information across all positions which is equal to the mutual information between position and spike count ($I(X,K)$). The power of this analytical technique is that: 1) informational content is calculated for each position; 2) the reliability of spike discharge across trials for each position is incorporated; and 3) there is no inherent bias for baseline firing rate. The spatial boundary of each position ($x_i$) was 5 cm in the direction of travel of the rat by 12 cm, which is the width of the track. There were 73 total positions, and 45 were encountered on any given traversal from the start to goal. Maps of the $I_{\text{pos}}(x_i)$ for each position are shown for this cell (Fig. 2A, bottom). The field traveling IN was associated with a peak in $I_{\text{pos}}(x_i)$ of 1.02 bits, and the field traveling OUT was associated with a peak in $I_{\text{pos}}(x_i)$ of 1.61 bits. Both fields were obviously dependent on the direction of travel as the cell did not fire in the opposite direction.
The degree to which ‘place fields’ reflected discrete changes in firing rate was assessed by quantifying field width as well as the abruptness of change from the baseline firing rate to the peak of in-field firing rate. Trials in which the rat traveled to the goal location via the same sequence of path segments were grouped (Fig. 2A; black line). The position data for these trials were linearized and the firing rate for each position is shown (Fig. 2B). A Gaussian function, constrained by the peak firing rate position \(x_i\) and average firing rate \(y_i\) was fit to the linearized firing rate data and the full width at half height (FWHH) of the curve fit was used to quantify the size of the field. The slope, at half height, (or ‘SHH’) of the same Gaussian function was taken as a measure reflecting the abruptness with which peak in-field firing rate was achieved. FWHHs for the firing fields on the IN and OUT paths were 28.0 cm and 34.1 cm, respectively. SHHs for the same IN and OUT firing fields were 0.74 Hz/cm and 0.55 Hz/cm, respectively. \(I_{pos}(x_i)\) for each position is also shown for comparison.

Using only the firing rate criterion, cell 2 had one field traveling IN and two fields traveling OUT (Fig. 2C). It is not uncommon for a CA1 ‘place cell’ to have multiple fields in the same environment (Gothard et al. 1996), and 7 out of 42 CA1 cells with fields had multiple fields on the same path. When analyzed for informational content, the field on the IN path was associated with a peak in \(I_{pos}(x_i)\) of 1.41 bits. Field A on the OUT path was associated with a peak in \(I_{pos}(x_i)\) of 0.69 bits, and field B on the OUT path was associated with a peak in \(I_{pos}(x_i)\) of 0.91 bits (Fig. 2C). The somewhat lower information values associated with fields A and B may be attributable to the fact that the response was approximately the same (~ 8 Hz) at each location. From the perspective of an ideal observer, a firing rate of 8 Hz on the IN path provides a high degree of
information that the animal is located at one specific location; however, a firing rate of 8 Hz on the OUT path only provides information that the animal is at one of two locations.

For the population of CA1 principal cells (n=74), 61 total fields from 42 cells were identified according to the firing rate definition. According to a the information metric (Skaggs et al. 1993) commonly used in the field (see methods), these neurons provided, on average, 1.86 bits of information per spike. Note that the information values derived from the two methods (Skaggs et al. 1993 versus Olypher et al., 2003) are not directly comparable. The mean amount of information per spike (1.86 bits) is consistent with what has been previously reported for neurons having a highly place-specific spike discharge (Frank et al. 2000; Frank et al. 2001; Hargreaves et al. 2005). With the newer method applied to all fields, the average peak in $I_{pos}(x_i)$ was 1.16 bits and for 95% of the fields the peak $I_{pos}(x_i)$ was greater than 0.65 bits. The average size (FWHH) of the fields was 30.9 cm and 95% of the fields were less than 57 cm in size. These location-specific positional information values obtained from classically identified CA1 ‘place cells’ were used to define and quantify spatial firing fields. Therefore, in this environment and using the positional information measure, a discrete field was deemed to exist when $I_{pos}(x_i)$ exceeded 0.65 bits and the spatial extent of the place field was less than 57 cm. Notably, there were no false-positive identifications of a field. Of the CA1 cells that lacked a field according to the firing rate criterion, none provided more than 0.65 bits of positional information for any position.

*Interneurons with discrete ON and OFF fields*
Having established the location-specific information content of CA1 principal cells, the informational content of interneurons was quantified for comparison. In contrast to principal cells, interneurons fire continuously while an animal is traversing a path, as shown for a representative interneuron (Fig. 3A). The average firing rate of this cell across all positions was 20.1 Hz. For this interneuron, there were two obvious places (field A and field B) on the OUT path where the firing rate was noticeably different than that of all other positions. At field A, the rate decreased to 2.2 Hz and at field B the rate increased to 40 Hz. The discrete decrease in activity at field A provided 1.23 bits of positional information, and the discrete increase in rate at field B provided 0.68 bits of positional information. Hereafter these fields will be referred to as OFF-fields and ON-fields respectively. The OFF field is enlarged (inset, top right) for visualization purposes. Both fields were dependent on the direction of travel of the rat. Directionality was quantified using the formula given in the methods (field A = 1.32; field B = 1.01). A value of 0 indicates that the firing rate was the same traveling IN or OUT, and a value of 0.5 indicates the firing rate was twice as large in one direction versus the other direction.

Linearized data from two routes on the OUT path are shown to illustrate the calculation of the FWHH, SHH, and $I_{pos}(x_i)$ values obtained (Fig. 3B,C). The linearized average firing rate is shown (Fig. 3B). The decrease in rate at field A is more apparent in the linearized firing rate plot than in the two-dimensional rate map. Note that the field is independent of the preceding path segments (black route versus blue route). A Gaussian function constrained by the peak position ($x_i$) and average firing rate ($y_i$) was fit to the firing rate data for each field. The FWHH of field A was 21.1 cm and the FWHH of field
B was 24.4 cm. The abruptness with which peak in-field firing rate was reached, as measured by SHH, was 1.05 Hz/cm and 1.10 Hz/cm, respectively.

For the same neuron, the firing rate at each position on each trial is shown (Fig. 3C). For the black path (top plot), the firing rate at each position for each trial is shown from 0 Hz to the mean rate (20.1 Hz). As can clearly be seen in this plot, 1) the cell was reliably silent across most trials at field A and 2) the cell was silent predominantly only at that position. For the blue path (bottom plot) the firing rate at each position and each trial is shown color-coded from the mean to 40 Hz. In this plot it is obvious that, 1) the firing rate was near or above 40 Hz on most trials at field B and 2) firing rates near or above 40 Hz occur predominantly only at field B. In summary, this interneuron had two fields, one ON and one OFF, that yielded positional information values and field widths comparable to the two example CA1 principal cells shown in Fig. 2.

To further illustrate the spatial specificity and informational content of interneuron fields, 6 more interneurons (2 subicular, 1 dentate gyrus, and 3 CA1) recorded from 5 different animals are shown (Fig. 4). All peak $I_{pos(x_i)}$ values, FWHH, and SHH values for these interneurons fell well within the ranges of the same values calculated for CA1 principal neurons. The peak $I_{pos(x_i)}$ values of all fields are shown for each cell (Fig. 4A-F). The first subicular cell had an OFF field (A) and an ON field (B) traveling OUT (Fig. 4A). The second subicular cell had an OFF-field traveling OUT (Fig. 4B). The dentate gyrus interneuron had an OFF field (A) and an ON field (B) traveling OUT (Fig. 4C). The first CA1 cell had three OFF fields (A, B, C) traveling IN (Fig. 4D). The second CA1 cell had two ON fields (A, B) and two OFF fields (C,D) traveling OUT (Fig. 4E). The last CA1 cell had one ON field (Fig. 4F). The widths of
the fields ranged from 23.1 cm (SUB-1: B field) to 35.3 cm (SUB-1: A-field). SHH values ranged between 0.58 Hz/cm and 0.96 Hz/cm.

Contribution of movement velocity

The firing rate of principal neurons and interneurons can also be affected by changes in movement velocity (McNaughton et al. 1983); however, movement velocity did not contribute to the spatial firing fields of the interneurons shown thus far. The contribution of movement velocity to the variability in firing rate was quantified to ensure that interneuron fields were indeed related to the spatial location of the animal.

For the interneuron shown in Fig. 3 (black route going OUT), firing rate versus movement velocity was plotted and a linear least-squares analysis was applied (Fig. 5A). The coefficient of determination ($r^2$) was 0.01 indicating that only one percent of the variation in firing rate could be explained by movement velocity. In addition, the low firing rate associated with the OFF field (filled symbols) was not related to maximal or minimal movement velocities.

The firing rate of many interneurons is known, however, to be related to movement velocity, and our dataset supports this fact. Firing rate versus movement velocity was plotted for all cells and least-squares analysis was performed. For 32 out of 59 interneurons (dark gray bars: subiculum: n=20; dentate gyrus: n=7; CA1: n=5), movement velocity explained less than 10% of the variance in firing rate (Fig. 5B). Given the number of positions sampled (45) for a given traversal, $r^2$ values less than 10% indicate that there was not a statistically significant correlation between movement velocity and firing rate (see methods). The 32 velocity-insensitive cells were used for the
population analyses described in the ensuing section. The 7 example interneurons shown (Figs. 3, 4) were members of this subpopulation. Of the other 27 cells, 12 had spatial firing fields that reached the criteria of ‘place field’, but given that movement velocity contributed to the variability in firing rate, there was no unequivocal way to determine the relative contributions of position and movement velocity.

Interneuron fields versus principal cell fields: similarities and differences

The width, directionality, and location-specific positional information of interneuron and principal neuron fields were very comparable. Histograms of the peak $I_{pos}(x_i)$ for all interneuron (23 cells, 44 fields) and CA1 principal cell (42 cells, 61 fields) fields are shown (Fig. 6A). There was no statistical difference between the average peak in $I_{pos}(x_i)$ of interneuron (1.02 bits) and principal cell (1.17 bits) fields (Fig. 6D).

Histograms of field widths are shown (Fig. 6B), and the average widths of the fields for the two populations were nearly identical (Fig. 6E; interneurons 30.7 cm; principal cells: 29.8 cm). In-field firing rates were similarly dependent on the direction of travel of the rat. Histograms of directionality values for all fields are shown (Fig. 6C) and there was no significant difference between interneuron and principal cell fields.

One of the most salient features of CA1 principal cells is the abrupt change in firing rate observed as an animal enters a place field. To determine whether firing rate changes associated with interneuron firing fields were similarly abrupt, we determined the slope, at half-height, (SHH) of the Gaussian functions fitted to each individual firing field. Similar values ($P >0.05$) for interneurons 0.77 Hz/cm and principal cells 0.72 Hz/cm were observed (Fig. 6F). Therefore, based on these defining characteristics, we
find that the spatial firing fields of interneurons are as discrete, directional, and informative as the fields of CA1 principal cell fields. Subicular and dentate gyrus principal cells were comparable to the CA1 principal cells. There was no statistical difference (ANOVA) among the groups of principal cells regarding the average peak positional information ($I_{\text{pos}}(x_i)$) for a field, mutual information $I(X;K)$, size of a field, or SHH values.

While the individual fields of interneurons and principal cells were similar, the populations differed in the mean positional information across all locations. Mutual information between the position and spike count variables, $I(X;K)$, was greater for interneurons than principal cells (Fig. 7A: 0.26 bits versus 0.13 bits, $P < 0.01$, note that $I(X;K)$ is equal to the mean of all location-specific positional information values, $I_{\text{pos}}(x_i)$). It was initially speculated that this may be attributable to the fact that interneurons simply fire more spikes. However, when position was randomly shuffled, $I(X;K)$ was negligible for both populations (Fig. 7B). Interneurons also differed from principal cells in that they had, on average, more fields per cell (Fig. 7C: 2.2 versus 1.4 fields per cell, $P < 0.01$).

There was a weak, statistically insignificant correlation between total positional information content and the number of fields. Therefore, the increased number of fields per interneuron may have contributed, in small part, to the increased total informational content of interneurons, but cannot be the sole cause. In summary, interneurons and principal neurons provide a comparable amount of location-specific information at a given field, but interneurons actually provide more location-specific information on average across all locations.
DISCUSSION

The application of a recently developed measure of positional information (Olypher et al. 2003;) to the firing patterns of hippocampal and subicular excitatory and inhibitory neurons clearly demonstrated that a subset of inhibitory interneurons exhibit discrete spatial firing fields having the same fundamental features as the fields of CA1 principal cells. This metric also revealed that interneurons have OFF fields that are as discrete and informative as classic ‘place fields’ of principal neurons. Taken together, these findings suggest that some interneurons register allocentric space more discretely than previously thought, and that fine-scale inhibitory and disinhibitory local network actions contribute to the construction of principal neuron ‘place fields’.

The location-specific firing fields of interneurons were shown to be like the fields of principal neurons in four distinct ways. First, peak in-field positional information values were well within the range of the values obtained for CA1, DG, and SUB principal neurons. This indicates that the in-field firing rates for interneurons were as unique and reliable as the robust ‘all-versus-none’ in-field firing rates of principal cells. Second, the abruptness with which firing rates changed from field entry to the point of peak in-field discharge was comparable for the two cell types. Third, the place-specific firing fields of both principal neurons and interneurons were strongly dependent on the animal’s direction of motion. Thus, interneurons and principal neurons are alike in generating distinct spatial activity patterns for different routes taken through track-style environments. Last, and perhaps most importantly, interneuron and principal cell fields were of the same size indicating that the registration of allocentric position by interneurons bears the same fine-scale specificity as that of principal neurons.
There are at least three possible reasons why previous reports have not concluded that interneurons are capable of exhibiting location-specific activity that is on a par with that of principal neurons. First, reports directly comparing interneuron and principal cell spatial activity patterns have been based primarily on CA1 interneurons (Frank et al. 2001; Kubie et al. 1990; Marshall et al. 2002). The number of CA1 cells in our dataset was somewhat limited and there are reportedly anywhere from 10 to 16 different types of interneurons in CA1 (Somogyi and Klausberger 2005). Therefore, while there are CA1 interneurons that exhibit discrete ‘place fields’ (see figure 3, also see Ego-Stengel and Wilson, 2007), it cannot presently be determined exactly how prevalent this capacity is among CA1 interneuron subtypes. The majority of velocity-insensitive subicular and DG interneurons exhibited discrete fields, and it is possible that the fine-scale mapping of space by interneurons is a more prevalent in these regions. Thus, many interneurons of the hippocampal formation are capable of discretely encoding space, but a much more exhaustive survey is needed to characterize this property across hippocampal formation interneuron subtypes.

A second reason for the apparent contradiction is that the most commonly used spatial information theoretic metric (Skaggs et al. 1993) is only a global measure and does not quantify the informational content provided at each location. It also does not consider the reliability of a response across separate visits to a particular position, and it is best suited for detecting the place fields of neurons having very low mean firing rates (Frank et al. 2001). In contrast, the analysis used here characterizes the spatial information provided by neuronal activity at each location within the environment, it incorporates reliability, and it considers any firing rate deviation from any baseline rate as
potentially informative (Olypher et al. 2003). The analysis yields high information values for a given location when the discharge rate is both unique to that location and is reliably observed across multiple visits. These are the exact properties that characterize the spatially specific activity patterns of classic ‘place cells’ which have reliably high in-field firing rates that stand out against a background of near-zero firing rates.

Finally, the third possible explanation may be the pooling of velocity-correlated and velocity-uncorrelated neurons in previous experiments. In any given task, reliable changes in movement velocity tend to occur over specific regions of an environment. If a transition in movement velocity occurs over a long distance, it follows that the firing rate may exhibit a corresponding broad modulation in rate.

Since we have shown that interneuron spatial firing fields are as spatially discrete as those of principal neurons, it follows that interneurons may directly shape the place-specific firing fields of principal neurons. This may equally occur via inhibitory or disinhibitory processes. The intrinsic excitability of interneurons contributes to an elevated baseline firing rate which enables them to discretely register spatial information by either activity maxima or minima. In the case of an OFF field, the discrete decrease in inhibitory input to a principal cell may in theory directly produce a field by enabling even a non-specific excitatory input to evoke suprathreshold events at that position. From an engineering standpoint, the discrete decrease in inhibitory input could also act as an ‘AND’ gate with like spatially-specific excitatory inputs (Klyachko and Stevens 2006). The discharge rate of a principal cell at any given position could therefore be dependent on both a specific increase in excitatory input and a specific decrease in inhibitory input to that cell.
Recent findings suggest that ON fields of interneurons reflect excitatory input from one or more principal cells (Marshall et al. 2002; Klausberger et al. 2005; Maurer et al. 2006). Such data is consistent with our finding that interneuron ON fields are as spatially discrete as those of principal cells. Together, these findings suggest that interneuron ON fields are largely driven by inputs from single principal cells or by groups of principal cells sharing identical spatial registers. Irrespective of the mechanism by which ON fields are produced, they should effectively decrease the probability of spiking in their principal neuron targets. In this way, interneuron ON fields could serve to maximize the segregation of principal neurons into active and inactive groups and thereby maximize the specificity with which principal neurons register position in the environment.

Alternatively, if an interneuron contacts other inhibitory inputs, the ON field response of an interneuron could actually facilitate the ON field response of a principal cell by indirectly providing disinhibition (Tsodyks et al. 1997). This may be especially true if the synaptic target of an interneuron is the axon of a non-specific inhibitory input innervating the proximal dendrite of a principal cell. Proximal inhibitory inputs may effectively compartmentalize a principal cell by shunting distal excitatory inputs. It follows that spatially discrete inhibition of those proximal inhibitory inputs can effectively de-compartmentalize a principal neuron and facilitate the conduction of distal excitatory inputs known to be important for place cell activity (Ang et al. 2005; Brun et al. 2002; Kocsis et al. 1999). Thus, interneuron ON field responses could, like OFF fields, effectively act as an ‘AND’ gate for distal excitatory inputs which share the same spatial specificity.
The electrophysiological properties and connectivity patterns of several interneuron subtypes in the hippocampus, entorhinal cortex, and subiculum strongly indicate that they are positioned to play a prominent role in generating the discrete spatial firing fields of principal neurons (Freund and Buzsaki 1996). For example, one subtype selectively innervates specific dendritic segments of principal cells suggesting that they serve to shunt specific afferent inputs (Han et al. 1993), and basket and chandelier interneurons may potently inhibit action potential generation in principal neurons via powerful synapses at the soma and axon initial segments (Somogyi et al. 1983a; Somogyi et al. 1983b). In vitro work demonstrates that interneurons strongly regulate the bursting behavior of principal neurons of the subiculum (Menendez de la Prida 2003). The activity of single interneurons can potently suppress activity in excitatory neurons (Cobb et al. 1995) and activity bursts of CA1 principal cells may be amplified by selective disinhibition (Klyachko and Stevens 2006). Basket and chandelier interneurons have previously been proposed to be critical in the timing of pyramidal neuron action potentials (Buzsaki and Chrobak 1995), and a recent work examining the timing of cholecystokinin-expressing neurons relative to the population theta rhythm suggests a role for this interneuron subtype in differentiating sub-groups of pyramidal neurons forming neuronal assemblies (Klausberger et al. 2005). Thus, the hypothesis that interneurons direct the fine-scale spatial specificity of principal cell field is consistent with anatomical and in vitro data.

Currently, there is no in vivo data detailing the dynamics of the inhibitory and excitatory synaptic inputs underlying the ‘place field’ responses of principal cells. In sensory systems and neocortex, where it is much easier to combine in vivo intracellular
recordings with the presentation of relevant sensory stimuli, a variety of inhibitory input
dynamics have been found to underlie the response tuning of individual neurons (Monier
et al. 2003; Wehr and Zador 2003; Wilent and Contreras 2005). The inhibitory input to a
cell can be exquisitely tuned for the preferred stimulus (Ferster 1986; Wehr and Zador
2003), but a diversity of tuning combinations are also encountered (Monier et al. 2003)
and preferred responses may also be associated with decreased inhibition (Fried et al.
2005; Rao et al. 2000). Thus, the possible roles of interneurons in shaping the spatial
firing fields of principal cells discussed here is consistent with the known functional role
of interneurons in neocortex.

While it remains to be determined whether the shape of principal cell place fields
is indeed critically dependent on the fine-scale positional firing patterns of interneurons,
it is notable that alterations in the spatial firing properties of interneurons and principal
cells tend to occur in parallel. For instance, physical restraint depresses interneuron
discharge and abolishes spatially selective discharge of CA1 principal cells (Foster et al.,
1989). The time courses for novelty-induced depressions in CA1 interneuron firing rates
and changes in the accuracy of principal cell based reconstruction of position are similar
(Wilson and McNaughton, 1993). Regions of an environment undergoing the greatest
novelty-induced change in interneuron firing rates overlap regions where the greatest
differences in principal cell spatial firing patterns are observed (Nitz and McNaughton,
2004). Finally, the spatial coherence of interneuron and principal cell activities are
similarly affected by pharmacological manipulation of cholinergic receptors (Brazhnik et
al., 2003).
The distinct afferent input patterns and architectures of hippocampal and subicular networks suggest that a thorough understanding of how spatial firing fields in the brain are generated is potentially attainable. Much is known concerning how environmental stimuli, self-motion information, and network oscillations affect the place-specific discharge properties of hippocampal and subicular excitatory neurons (Barnes et al. 1990; Eichenbaum et al. 1990; Ferbinteanu and Shapiro 2003; Knierim et al. 1995; McNaughton et al. 1983; O'Keefe and Conway 1978; Wilson and McNaughton 1993; Wood and Dudchenko 2003). In addition, recent work has identified differences in the form in which spatial information is registered across different sub-regions of the hippocampus, the subiculum, and the entorhinal cortex (Frank et al. 2000; Hafting et al. 2005; Knierim et al. 1995; Sharp and Green 1994). It is likely that sub-region specific transformations in the way that space is registered are more than simply a product of excitatory afferent input dynamics. The role of local networks is undoubtedly important and it has been shown here that location-specific inhibition and disinhibition is prominent within the hippocampal formation.

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FIGURE LEGENDS

Fig. 1. Delineation of putative principal cells and interneurons. Interneurons (grey box at left) had average firing rates greater than 15 Hz and extracellular spike widths that were less than 0.33 ms, and comprised 15.4% or all recorded neurons. Principal cells (grey box at bottom right) had average firing rates less than 15 Hz and extracellular spike widths greater than 0.32 ms. Subicular cells (circles), CA1 cells (triangles), and dentate gyrus cells (squares) are delineated. Cells that could not be classified are also indicated (black figures, white background).

Fig. 2. Spatial firing fields of two representative CA1 principal cells. A: Maps of firing rate and $I_{pos}(x_i)$ are shown for cell 1. Maps traveling IN are at left and maps traveling OUT are at right. This cell had one field traveling IN that was associated with a peak in $I_{pos}(x_i)$ of 1.02 bits, and one field traveling OUT that was associated with a peak in $I_{pos}(x_i)$ of 1.61 bits. Two routes, one on the IN rate map and one on the OUT rate map, are indicated (black lines). B: Data from the trials in which the route traversed to the goal location via one of those two routes were used to generate an average firing rate at each position for each route. The data is presented in a linearized fashion. $I_{pos}(x_i)$ values for each position are shown below. A Gaussian function was fit to the linearized firing rate data, and the full-width half-height of the fits were used to quantify the width of the fields. The field traveling in was 28.0 cm in width and the field traveling OUT was 34.1 cm in width. C: Maps of firing rate and $I_{pos}(x_i)$ are shown for cell 2. This cell had one field traveling IN (left) that was associated with a peak in $I_{pos}(x_i)$ of 1.41 bits and two
fields traveling OUT (right) that were associated with peaks in $I_{pos}(x_i)$ of 0.69 (A-field) and 0.91 bits (B-field).

Fig. 3. Spatial firing fields of a representative interneuron. A: Firing rate map and $I_{pos}(x_i)$ map are shown for OUT traversals, and two fields (A,B) are indicated. Top inset at right highlights the rate decrease at the OFF field (A) and bottom inset at right is the firing rate map and $I_{pos}(x_i)$ map for IN traversals. Two complete routes (black and blue lines) are illustrated. Note that the rat traversed through both field A and B when he took the blue route and only traversed through field A when he took the black route. B: For each route, trials in which the rat traversed to the goal location via that route were averaged and the average firing rate at each position is shown in a linearized fashion. Gaussian functions were fit (red dashed lines) to the linearized firing rate data. The OFF field (A) was 21.1 cm in width and the ON field was 24.4 cm (B). Note that the decrease in rate at the OFF field (A) was independent of route. C: To illustrate the reliability and uniqueness of the responses at fields A and B, the firing rate for each position on every trial is shown. The firing rate is shown from 0 Hz to the mean (20.1 Hz) for the black route (top) and is shown from the mean to 40 Hz for the blue route (bottom).

Fig. 4. Maps of firing rate and $I_{pos}(x_i)$ for 6 more velocity-insensitive interneurons. 2 SUB (A,B) 1 DG (C), and 3 CA1 interneurons (D,E,F) are shown. The fields are indicated on the firing rate maps by a capital letter. Peak $I_{pos}(x_i)$ values of each field are indicated on the corresponding map of $I_{pos}(x_i)$. 
Fig. 5. Contribution of movement velocity to firing rate. A: Firing rate versus movement velocity was plotted using the data from the interneuron depicted in Figure 3 on the black route traveling OUT. A least-squares analysis was performed and the coefficient of determination ($r^2$) was 0.01 indicating that only 1% of the variability in firing rate could be explained by changes in movement velocity. Filled symbols represent data from the OFF field. B: The same analysis was applied to all interneurons on all paths and a histogram of the $r^2$ values is shown. For 32 (dark gray) out of the 59 cells, movement velocity contributed less than 10% of the variability in firing rate. For these cells, the correlation between movement velocity and firing rate was not statistically significant.

Fig. 6. Similarities between interneuron and CA1 principal cell fields. Interneuron data (light gray bars) are shown relative to principal cell data (dark black bars) for four features of firing fields: peak $I_{pos(x)}$, field width, directionality, and speed of rate change between baseline and peak in-field firing rates. A: Histograms of the peak $I_{pos(x)}$ values for all interneuron and CA1 principal cell fields are shown. B: Histograms of the widths of all interneuron and CA1 principal cell fields. C: Histograms of the directionality of all interneuron and CA1 principal cell fields. The average directionality of interneuron fields was 1.02 and the average directionality of CA1 principal cell fields was 0.99. This difference was not significant. D: The average peak in $I_{pos(x)}$ was 1.03 bits for interneurons (Int) and 1.18 bits for principal cells (Princ). E: The average width of interneuron (31.8 cm) and principal cell fields (31.2 cm) were quite similar. F: The
average abruptness of the field, measured as the slope of the Gaussian fit at half height, was similar for interneurons (0.77 Hz/cm) and principal cells (0.72 Hz/cm).

Fig. 7. Differences between interneurons and CA1 cells. Interneuron data (gray bars) are shown relative to principal cell data (black bars). A: Across all positions, the average positional information, I(X,K), provided by interneurons was double that of CA1 principal cells (0.26 bits versus 0.13 bits, P < 0.01). B: This difference was not attributable to an increased number of spikes because when position was randomly shuffled, I(X,K) values were negligible for both populations. C: For cells with fields, interneurons had more fields per cell (2.2 versus 1.4, P < 0.01) than CA1 principal cells.
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