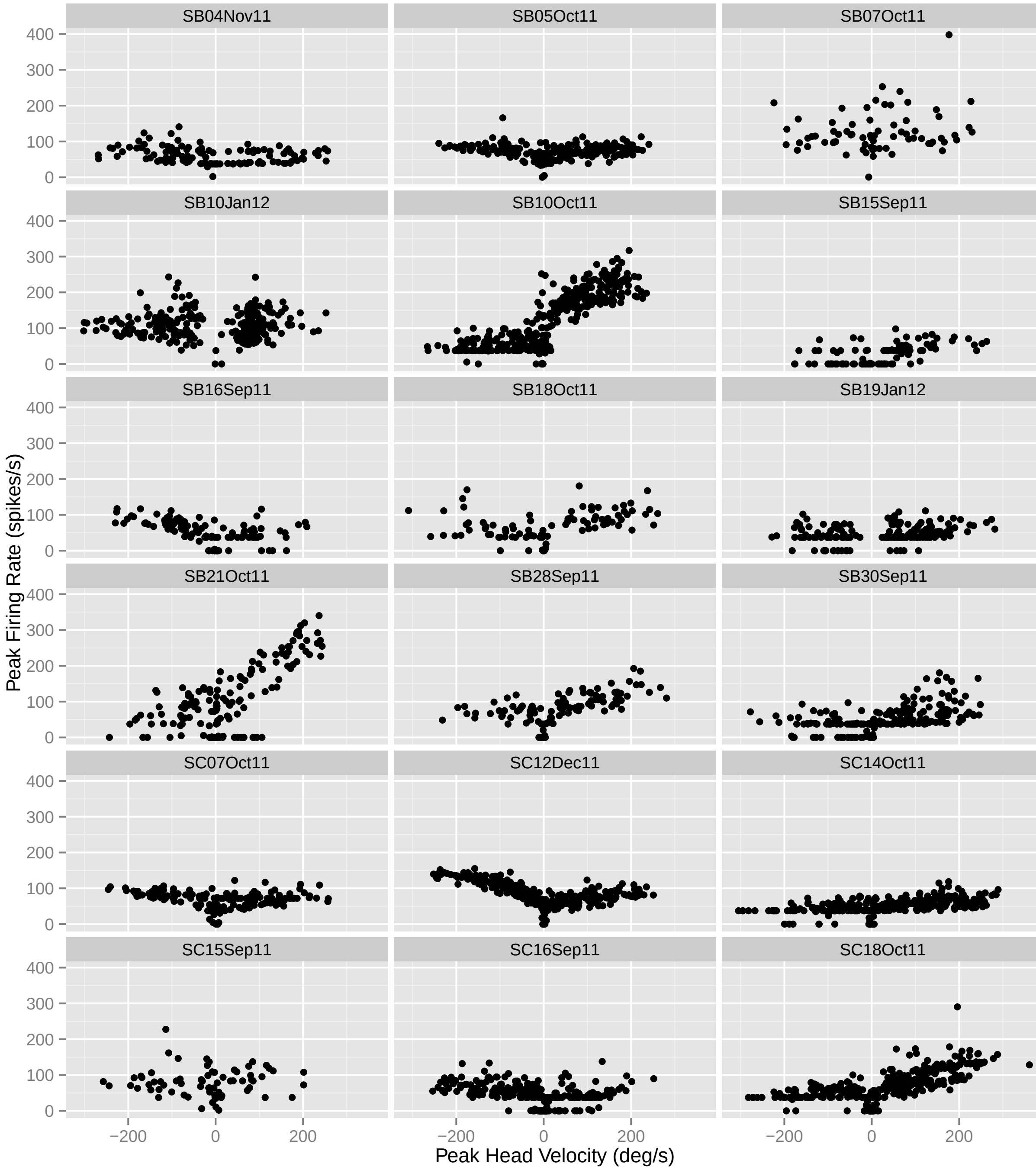
NRG Recording Analysis

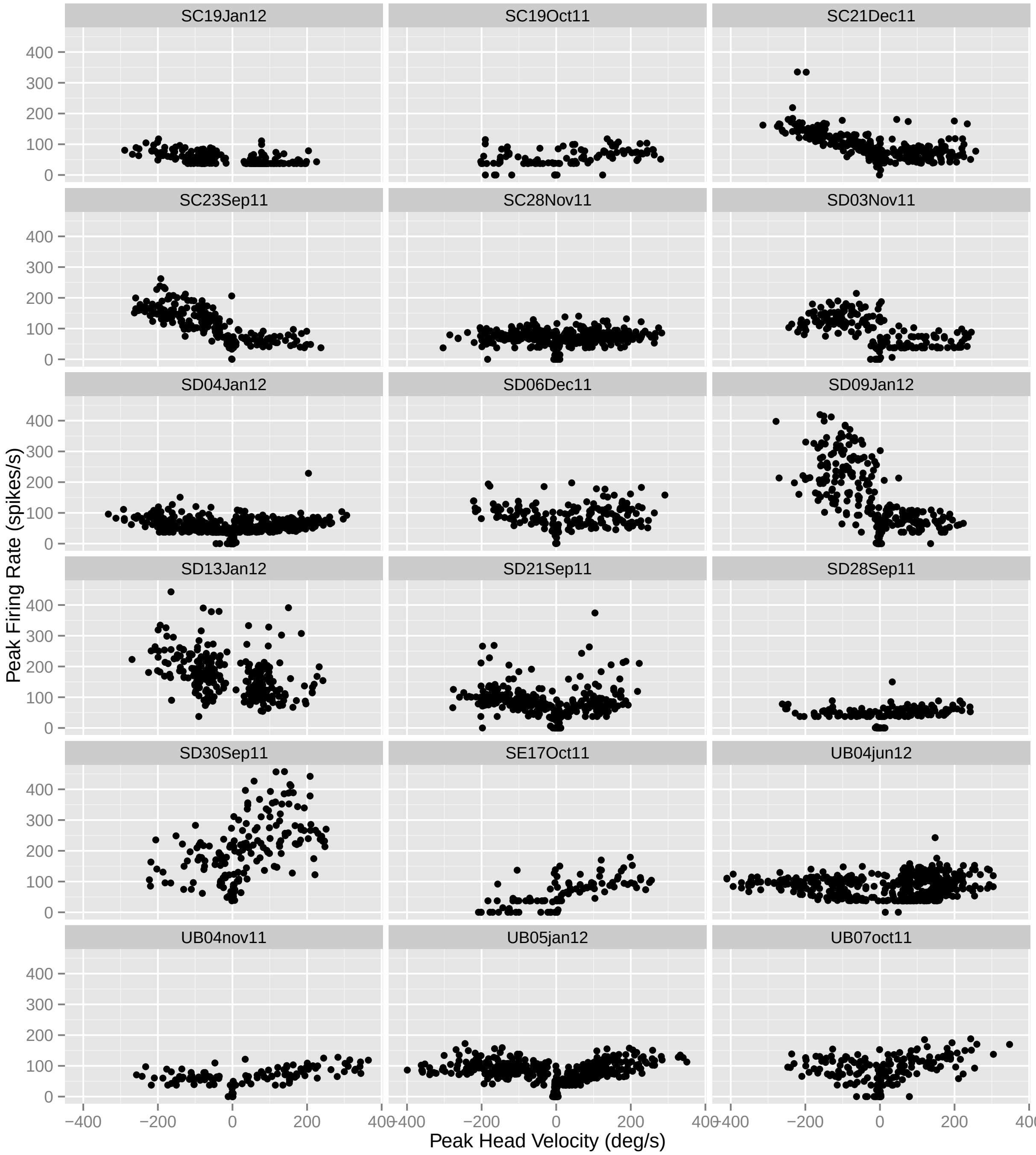
Results

We isolated 163 neurons (94 from S and 69 from U) in NRG while monkeys performed head-unrestrained gaze shifts and gaze pursuit tasks. We chose 51 of these neurons for further analysis in this report, based on apparent head-movement-related activity as perceived by the researchers during recording, and the recording of at least 50 successful trials while isolation was maintained. The behavior tasks that our monkeys performed provided us with a large variety of head movements to investigate. Controlling initial eye position provided us with examples of pursuit and gaze shifts of similar velocities and amplitudes with varying amounts of head contribution. This provided us with the ability to identify neurons with head-related activity during recording. For offline analysis, we can compare the firing rate of the neurons to the actual head and eye kinematics on a trial-by-trial basis. While our focus was on horizontal movements, we recorded the vertical positions of the gaze, eyes and head at all times.

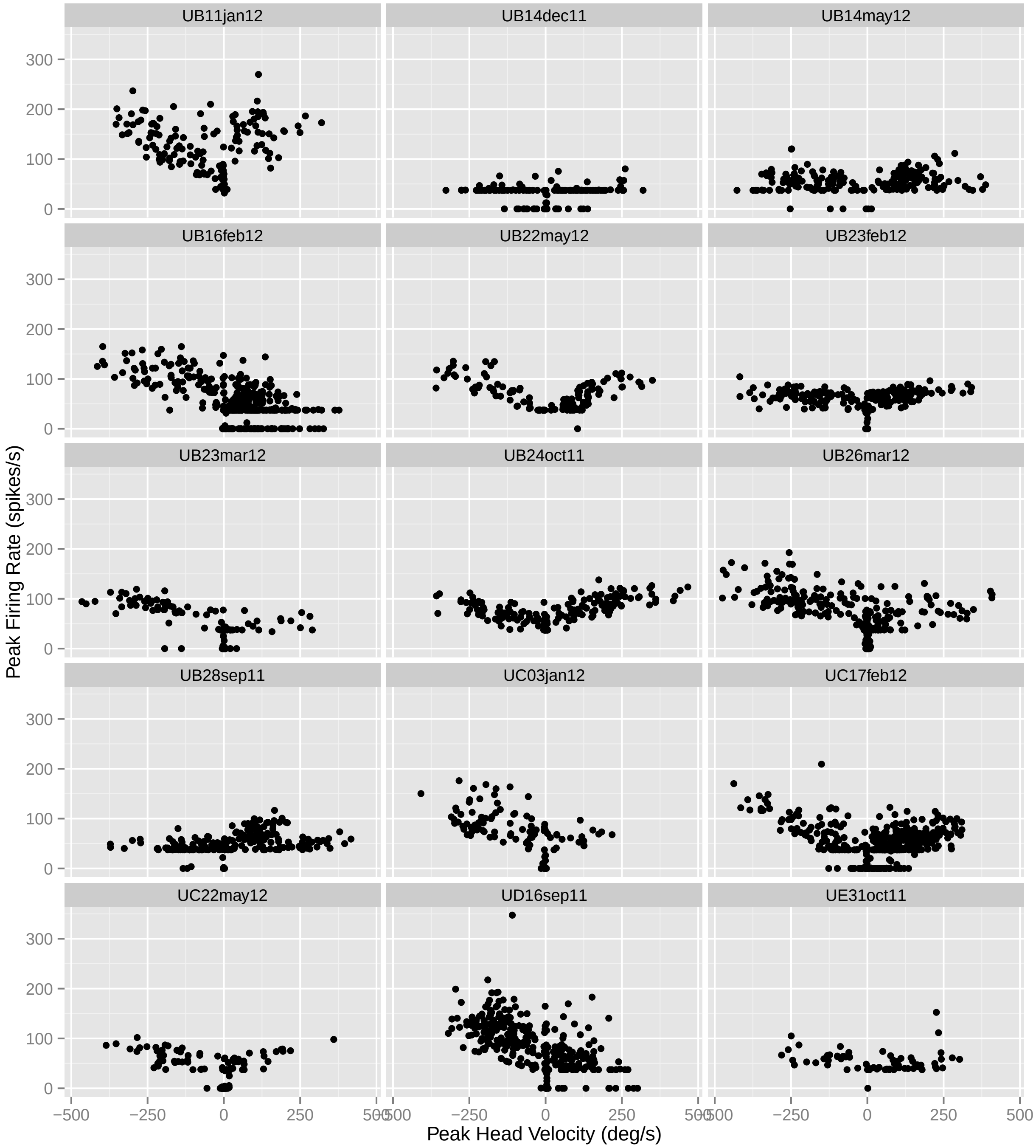
Since we have preselected our neurons based on apparent task-related activity, we first look for evidence that the rate of activity is correlated with the velocity of head movements. In the following figure, we plot the peak velocity of the head (negative values indicate that the fastest head movement was leftward), and the peak discharge rate of the cell during each trial. We show data observed during all trial types. For pursuit trials, we restrained our search for the peak values to the first trajectory only, to avoid including effects from vertical or oblique movements.



SB04Nov11
SB05Oct11
SB07Oct11
SB10Jan12
SB10Oct11
SB15Sep11
SB16Sep11
SB18Oct11
SB19Jan12
SB21Oct11
SB28Sep11
SB30Sep11
SC07Oct11
SC12Dec11
SC14Oct11
SC15Sep11
SC16Sep11
SC18Oct11
Peak Firing Rate (spikes/s)
Peak Head Velocity (deg/s)
0
100
200
300
400
−200
0
200

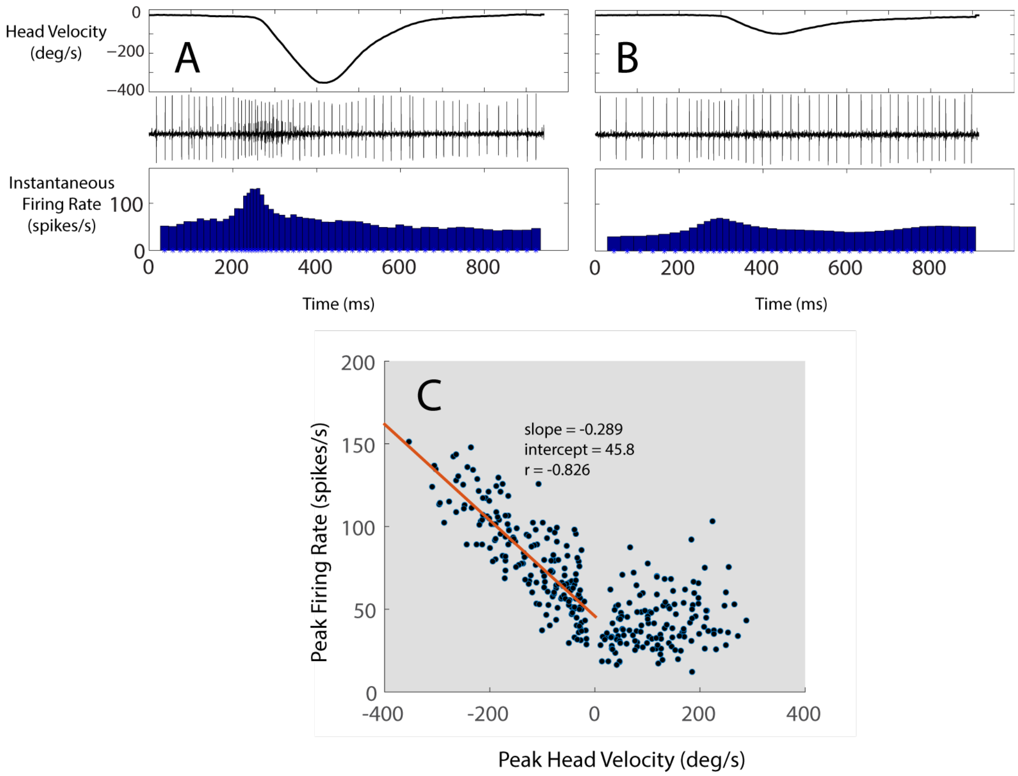


SC19Jan12
SC19Oct11
SC21Dec11
SC23Sep11
SC28Nov11
SD03Nov11
SD04Jan12
SD06Dec11
SD09Jan12
SD13Jan12
SD21Sep11
SD28Sep11
SD30Sep11
SE17Oct11
UB04jun12
UB04nov11
UB05jan12
UB07oct11
Peak Firing Rate (spikes/s)
Peak Head Velocity (deg/s)

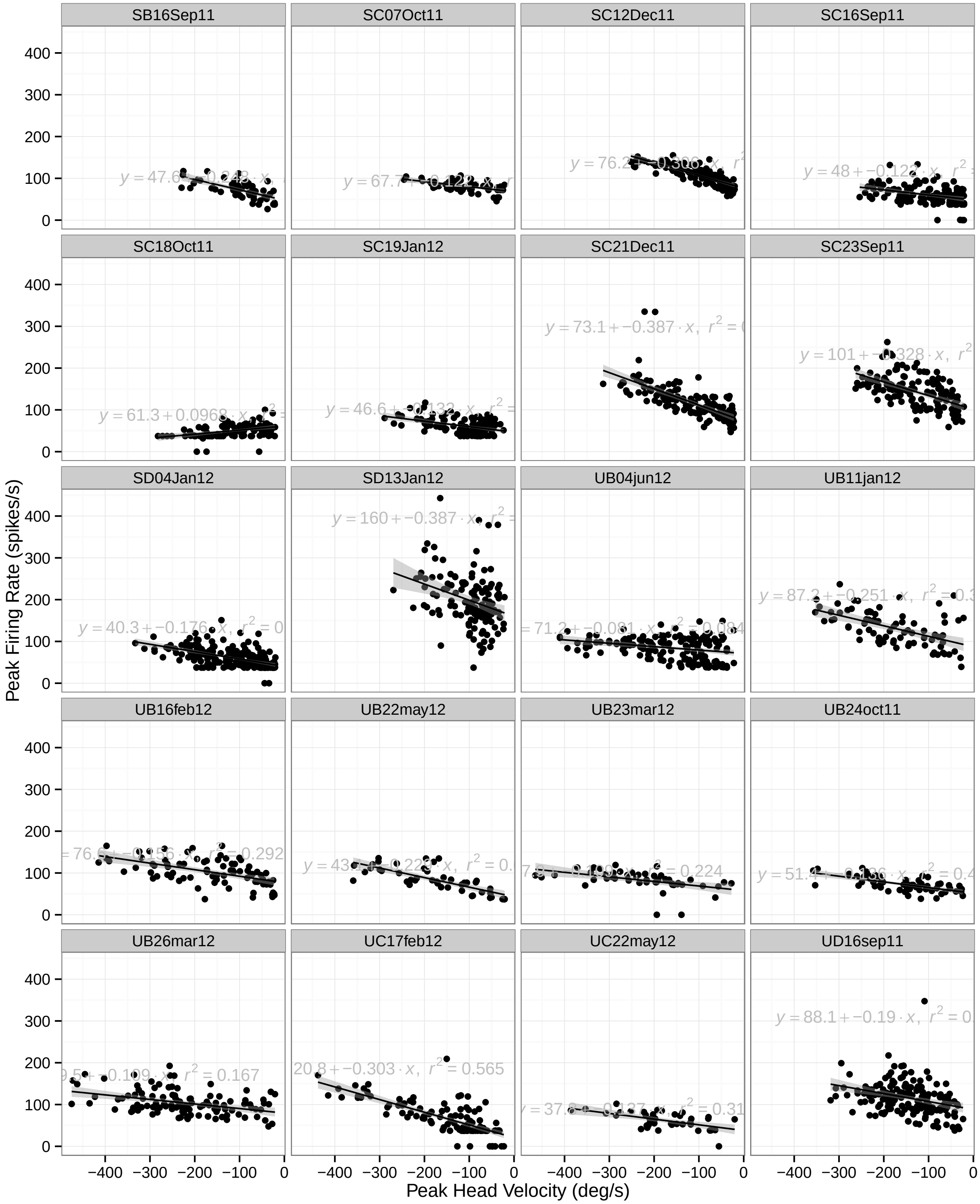


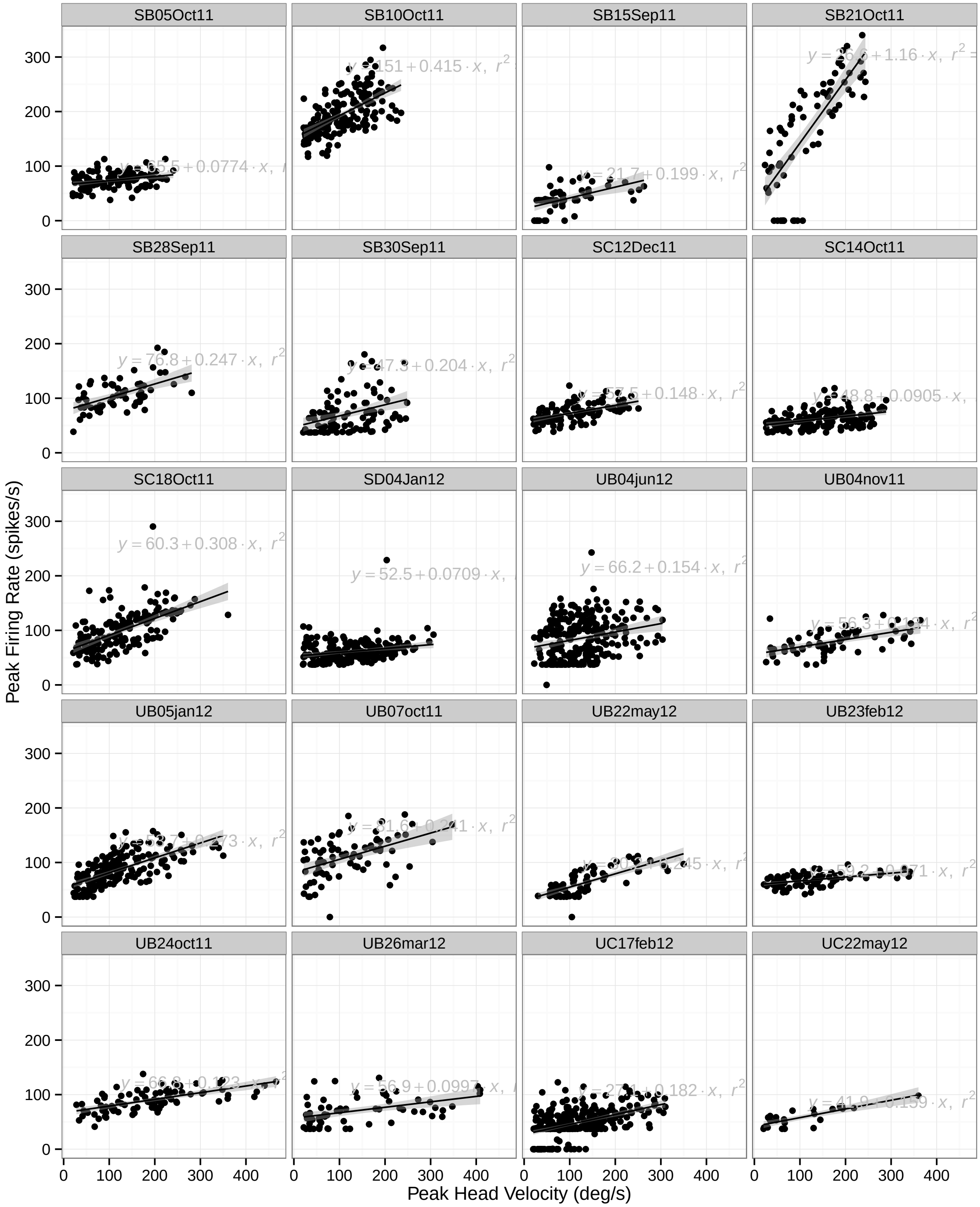
From the figure above, it is apparent that we have a heterogenious sample of neurons. The peak firing rate of many cells never exceeds 200 spikes/s, while some have a peak firing rate greater than 400 spikes/s. There seem to be correlations between the peak head velocity and peak firing rate in many neurons, and this correlation appears to be directionly selective.

For our first statistical test, we use linear regression to find the relationship between peak head velocity and peak firing rate for each neuron. We fit leftward and rightward movements using separate models. In the figure below, we show an example cell demonstrating this process. Panel 1A shows the head velocity and corresponding activity of the neuron during a fast, leftward head movement, while 1B shows the same during a slower head movement. For each trial, we record the peak head velocity and the peak firing rate of the neuron, which are plotted in 1C. We fit a linear regression model for the relationship between peak firing rate and peak velocity in each direction. For the example neuron shown in 1C, this regression was significant ($p<0.001$) for leftward movements only.

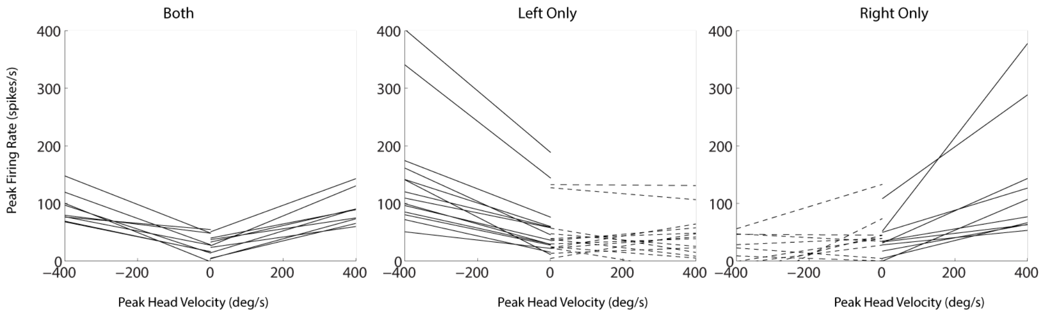


In the figure below, we plot the 20 neurons with significant leftward regressions, followed by the 20 cells with signficant rightward regressions. We found that 9 cells had signficant regressions in both directions.


SB16Sep11
SC07Oct11
SC12Dec11
SC16Sep11
SC18Oct11
SC19Jan12
SC21Dec11
SC23Sep11
SD04Jan12
SD13Jan12
UB04jun12
UB11jan12
UB16feb12
UB22may12
UB23mar12
UB24oct11
UB26mar12
UC17feb12
UC22may12
UD16sep11
Peak Firing Rate (spikes/s)
Peak Head Velocity (deg/s)



As a summary, we show the regression lines from all of the above neurons on the same axes, separated by direction preference.

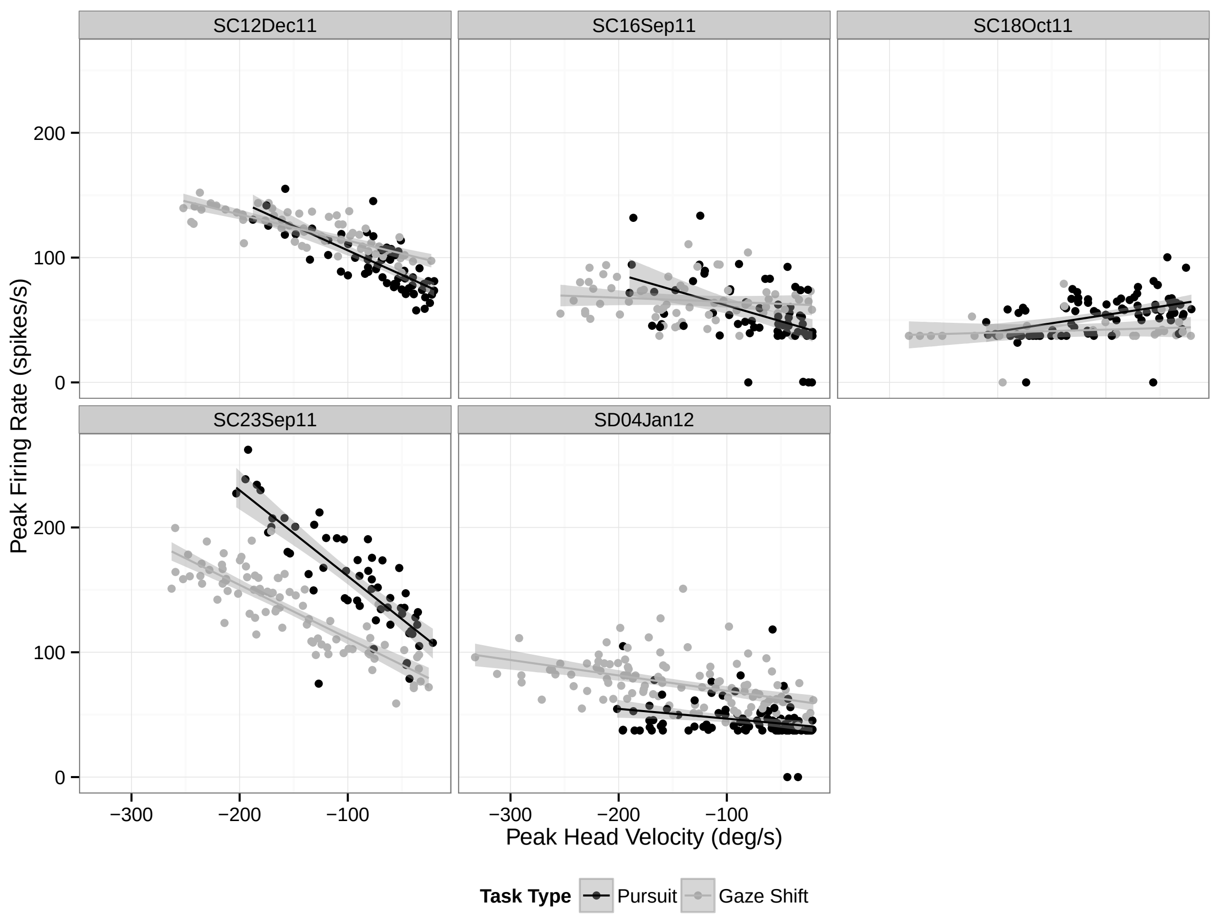


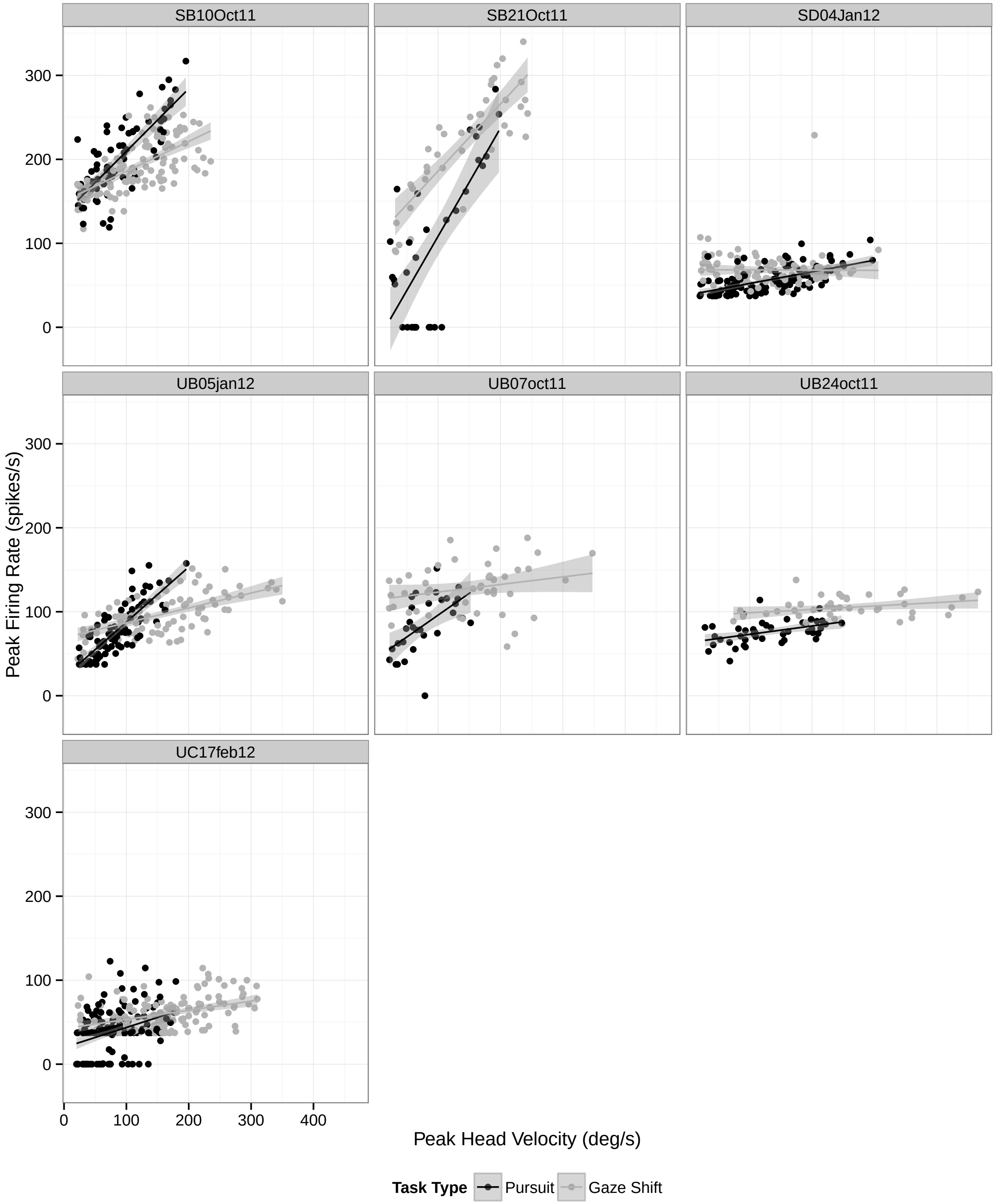
Of the cells with significant regressions for all head movements, we further tested for the significance of the type of task that was used to elicit the head movements on this relationship. We fit the model

$$Fr_{peak} = x_0 + x_1 H_{peak} + x_2 T_{type} + x_3 H_{peak} * T_{type},$$

where Fr_{peak} is the peak firing rate, H_{peak} is the peak head velocity, and T_{type} is the task (delayed gaze shift or head-unrestrained pursuit) that was required during each trial,and the $*$ indicates an interaction between the two parameters. A significant x_2 term indicates a difference in the intercepts for the relationship between peak head velocity and peak firing rate for the trial types, while a significant x_3 term indicates a difference in slope between the two.

In the figures below, we plot data from the 5 cells with significant effects of the task type on either the slope or intercept of the fit for leftward head movements, followed by the 7 cells significant during rightward movements.



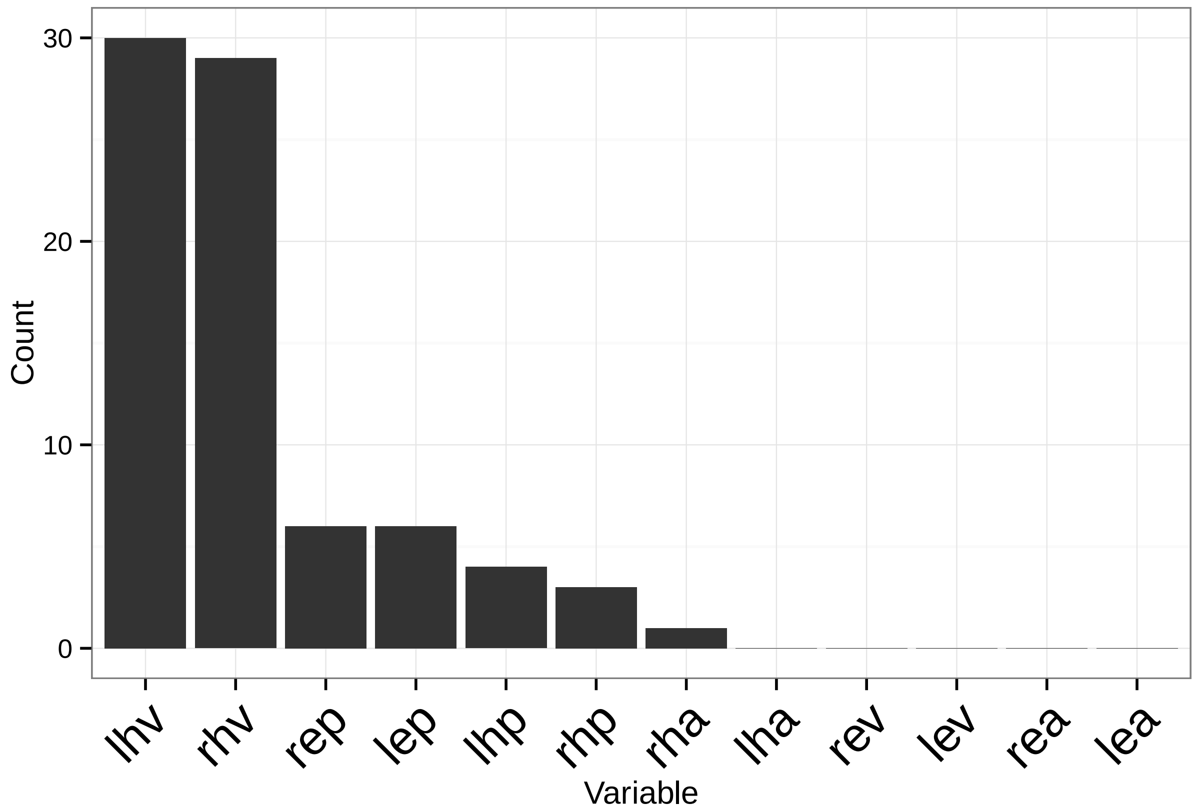


Following the methods described above (see Methods: Modeling), for each cell, we generated a model to predict the firing rate of the neuron in terms of eye and head position, velocity and acceleration. Each model includes only terms that increase the R^2 of the model by 0.05 or more. When describing velocity and position, we typically use negative values to indicate leftward, but for these models, we treat leftward and rightward values as separate variables. The table below shows the resulting best model for each cell, the shift, or latency between neural activity and behavior that provides the best model (measured by R^2) and the R^2 of the resulting model compared to the real neural activity.

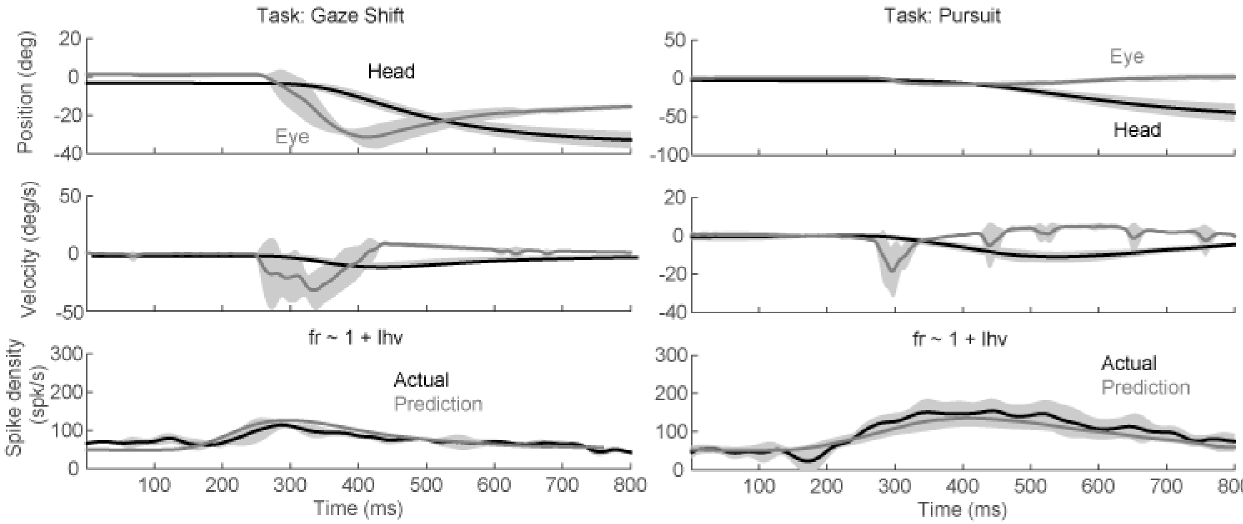
Neuron	shift	rsquared	f
SB21Oct11	120	0.77	fr ~ 1 + rhv + rep
UB21dec11	60	0.70	fr ~ 1 + lep
UB22may12	70	0.64	fr ~ 1 + rhv + lhv
SE17Oct11	150	0.58	fr ~ 1 + rhv
SB10Oct11	170	0.58	fr ~ 1 + rhp + rhv
UC22may12	80	0.57	fr ~ 1 + rhv + lhv
SC23Sep11	130	0.47	fr ~ 1 + lhv
UBA4jun12	90	0.46	fr ~ 1 + rhv + lhv
SD09Jan12	130	0.41	fr ~ 1 + lhv
UB23mar12	80	0.40	fr ~ 1 + lhv + rep
SC12Dec11	70	0.40	fr ~ 1 + lhv
UB16feb12	90	0.40	fr ~ 1 + lhv
UB05jan12	60	0.39	fr ~ 1 + lhp + lhv + rha
SB15Sep11	110	0.37	fr ~ 1 + rhv
UB28sep11	20	0.35	fr ~ 1 + rhp + rhv + rep
SD03Nov11	160	0.34	fr ~ 1 + lhv
SC18Oct11	40	0.33	fr ~ 1 + rhv + lep
SB16Sep11	70	0.32	fr ~ 1 + lhv
UD16sep11	130	0.32	fr ~ 1 + lhv
UB04nov11	70	0.31	fr ~ 1 + rhv + lhv
UBB4jun12	130	0.30	fr ~ 1 + rhv + lhv
SB18Oct11	70	0.30	fr ~ 1 + rhv
UB26mar12	80	0.30	fr ~ 1 + lhv
UE31oct11	40	0.29	fr ~ 1 + rhv + lhv
SC21Dec11	130	0.29	fr ~ 1 + lhv
SC07Oct11	80	0.28	fr ~ 1 + lhp + lhv
SD13Jan12	190	0.27	fr ~ 1 + lhv
UC17feb12	100	0.26	fr ~ 1 + lhv + rep
SC16Sep11	60	0.26	fr ~ 1 + lhv + lep
UB24oct11	50	0.24	fr ~ 1 + rhv
UC03jan12	110	0.23	fr ~ 1 + lhv + rep
UB14may12	100	0.23	fr ~ 1 + rhv + lhv
SC19Oct11	70	0.22	fr ~ 1 + rhv
SD30Sep11	200	0.22	fr ~ 1 + rhp + rhv
SC28Nov11	110	0.21	fr ~ 1 + lhv + lep
SC14Oct11	180	0.20	fr ~ 1 + rhv
SD04Jan12	60	0.20	fr ~ 1 + rhv
SC19Jan12	190	0.20	fr ~ 1 + lhv
SB28Sep11	50	0.19	fr ~ 1 + rhv + lep
SD21Sep11	60	0.18	fr ~ 1 + rhv + lhv
SB05Oct11	80	0.17	fr ~ 1 + rhv + lhv
SB10Jan12	90	0.17	fr ~ 1 + lhv + lep
SB30Sep11	130	0.16	fr ~ 1 + rhv
SB19Jan12	120	0.16	fr ~ 1 + rhv
SD06Dec11	50	0.15	fr ~ 1 + rhv + lhv
SB04Nov11	90	0.15	fr ~ 1 + rhv + lhv
UB07oct11	80	0.14	fr ~ 1 + lhp + rhv
UB23feb12	50	0.13	fr ~ 1 + rhv
SD28Sep11	130	0.09	fr ~ 1 + rep
UB11jan12	40	0.06	fr ~ 1 + lhp

Neuron	shift	rsquared	f
SB07Oct11	200	0.05	fr ~ 1 + rhv
SC15Sep11	20	0.00	fr ~ 1
UB14dec11	20	0.00	fr ~ 1

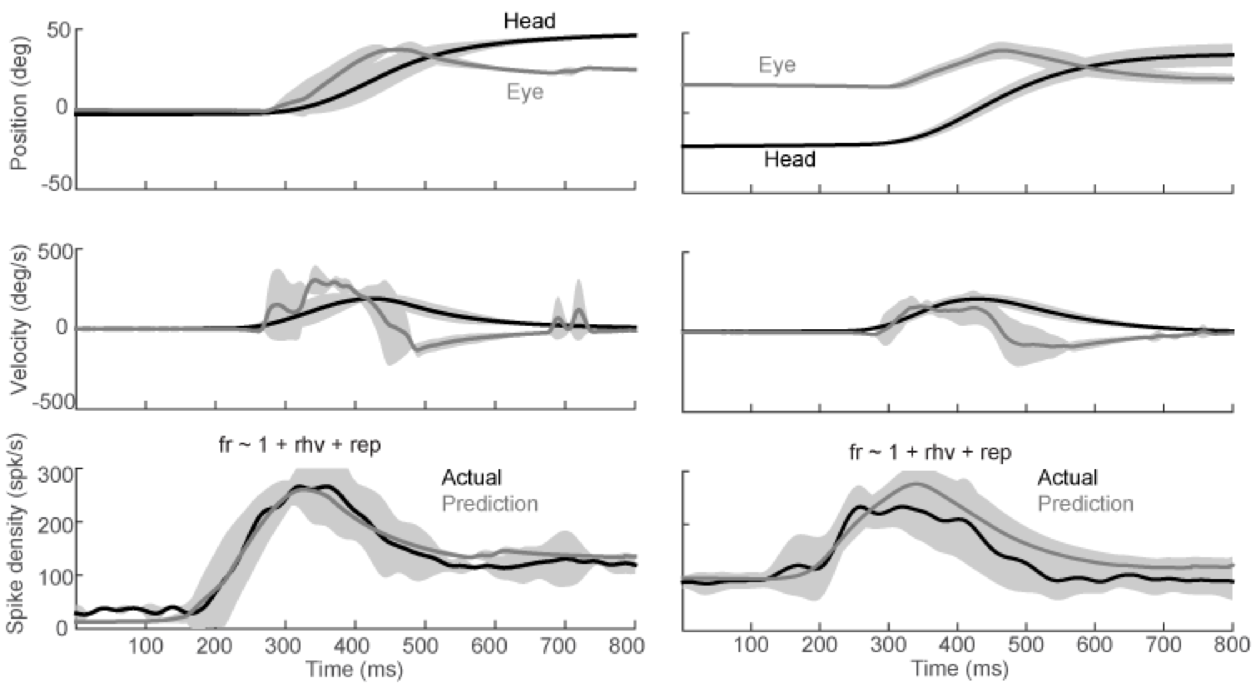
Breaking down the results shown in the above table, first we show the number of times each variable appears in any of the the final models.



It is clear that leftward and rightward head velocity are included more than any other varaibles, but we also see influence of head and eye position in several models. Only one model was improved significantly by the inclusion of head acceleration. In the figure below, we compare the model prediction of firing rate with the actual firing rate for one neuron. The model for this neuron uses a latency of 130 ms and predicts firing rate with an R^2 of 0.47 using only leftward head velocity. The stepwise fit procedure did not find any single term that would improve the R^2 by 0.05 or more, yet the model systematically underestimates firing rate during the gaze shift and overestimates firing rate during the pursuit task. This is consistent with the previous observation that the relationship between peak firing rate and peak head velocity was significantly different between tasks types for this neuron.



Below, we show the model prediction for a neuron that includes a significant eye position term. In the left panels, the eyes begin the trials in the center of the orbits, while in the right panels, the eyes begin deviated to the right in the orbits. The increased firing during fixation in this position is predicted by the eye position term in the model. Similarly, after the gaze shift, the firing rate is also elevated, corresponding with the eccentric eye position.



Because head position and eye position are often correlated, it may be possible to model activity equally well using either as a single parameter in the model, particularly for models with low R^2 values. We investigate this position-related activity further by isolating the periods of fixation before and after gaze shifts. We then fit the activity of each of the cells that included a position term in the stepwise fit above with the model:

$$Fr = x_0 + x_1 H_R + x_2 E_R + x_3 H_L + x_4 E_L$$

In the table below, for each neuron, we show the coefficient (x_{1-4}) with the greatest value using this method.

Neuron	rsquared	Highest.Coefficient	Position.Type
UB21dec11	0.95	7.96	Leftward.Eye
SB21Oct11	0.76	2.16	Rightward.Eye
SC18Oct11	0.58	0.85	Rightward.Head
SC28Nov11	0.20	1.05	Rightward.Eye
SB10Oct11	0.19	1.26	Rightward.Eye
UB05jan12	0.14	0.57	Rightward.Head
UC03jan12	0.11	0.39	Rightward.Eye
UB28sep11	0.11	0.42	Rightward.Head
SB28Sep11	0.10	1.27	Rightward.Head
SC16Sep11	0.10	0.71	Rightward.Eye
SC07Oct11	0.09	0.66	Rightward.Head
UC17feb12	0.08	0.17	Rightward.Head
UB23mar12	0.03	0.15	Rightward.Head

Although our focus is on horizontal movements, our data set included movements off of the horizontal axis. These movements give us the opportunity to assess the sensitivity of these neurons to oblique eye and head movements. In the table below, we show the results of allowing upward or downward movements to be included as variables in the model, using the same modeling procedure as above. In the table, we represent upward movements with u and downward movements with d. We restrict the table to show only the eight neurons that included a vertical component to the fit.

Neuron	shift	rsquared	f
UB28sep11	20	0.37	fr ~ 1 + rhp + rhv + uhv
SC21Dec11	130	0.34	fr ~ 1 + lhv + uhp
UC17feb12	100	0.31	fr ~ 1 + lhv + rep + uhv
SC19Oct11	70	0.36	fr ~ 1 + rhv + uhv + dep
SD04Jan12	60	0.26	fr ~ 1 + rhv + uhv
SB30Sep11	130	0.27	fr ~ 1 + rhv + uhv
SB04Nov11	90	0.10	fr ~ 1 + uhv
UB11jan12	40	0.14	fr ~ 1 + dhv