Supporting Information Appendix

Multiple timescales of neural dynamics and integration of task-relevant signals across cortex

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Model #	Model components
1	average response only
2	exogenous terms only
3	intrinsic autoregressive only
4	exogenous terms and intrinsic autoregressive
5	seasonal autoregressive only
6	exogenous terms and seasonal autoregressive
7	intrinsic and seasonal autoregressive
8	exogenous terms, intrinsic and seasonal autoregressive
9	reward-memory trace only
10	exogenous terms and reward-memory trace
11	intrinsic autoregressive and reward-memory trace
12	exogenous terms, intrinsic autoregressive and reward-memory trace
13	seasonal autoregressive and reward-memory trace
14	exogenous terms, seasonal autoregressive and reward-memory trace
15	intrinsic and seasonal autoregressive plus reward-memory trace
16	exogenous terms, intrinsic and seasonal autoregressive plus reward-memory trace
17	choice-memory trace only
18	exogenous terms and choice-memory trace
19	intrinsic autoregressive and choice-memory trace
20	exogenous terms, intrinsic autoregressive and choice-memory trace
21	seasonal autoregressive and choice-memory trace
22	exogenous terms, seasonal autoregressive and choice-memory trace
23	intrinsic and seasonal autoregressive plus choice-memory trace
24	exogenous terms, intrinsic and seasonal autoregressive plus choice-memory traces
25	reward- and choice-memory traces
26	exogenous terms plus reward- and choice-memory traces
27	intrinsic autoregressive plus reward- and choice-memory traces
28	exogenous terms, intrinsic autoregressive plus reward- and choice-memory traces
29	seasonal autoregressive plus reward- and choice-memory traces
30	exogenous terms, seasonal autoregressive plus reward- and choice-memory traces
31	intrinsic and seasonal autoregressive plus reward- and choice-memory traces
32	exogenous terms, intrinsic and seasonal autoregressive plus reward- and choice-memory traces

Table S1. List of all possible combinations of the models used to fit neural response and their main components. Exogenous terms refer to regressors included in the model to capture the effects of task-relevant signals on neural response.

Timescales	Cortical area	*p*-value	Cohen's *d*	d.f.	#task-relevant	#non task-relevant
Intrinsic timescales	LIP	0.63	0.03	111.29	124	68
	dmPFC	0.08	0.12	91.67	120	56
	dlPFC	0.43	0.05	226.84	170	131
	ACC	0.87	0.01	113.51	80	62
	All	0.06	0.14	654.39	494	317
Seasonal timescales	LIP	0.42	0.10	36.86	21	21
	dmPFC	0.22	0.13	49.41	48	30
	dlPFC	0.43	0.09	74.82	38	39
	ACC	0.27	0.10	59.66	31	31
	All	0.22	0.06	246.26	138	121
Reward-memory timescales	LIP	0.43	0.06	108.32	92	58
	dmPFC	0.97	0.003	64.32	74	41
	dlPFC	0.02	0.15	193.79	125	89
	ACC	0.88	0.01	102.09	69	50
	All	0.18	0.05	595.12	360	238
Choice-memory timescales	LIP	0.88	0.01	115.94	83	52
	dmPFC	0.12	0.14	98.10	85	34
	dlPFC	0.50	0.05	97.63	112	89
	ACC	0.06	0.22	32.92	41	31
	All	0.52	0.03	510.35	321	206

Table S2. Dependence of timescales on overall selectivity to task-relevant (reward outcome and choice) signals. Reported are *p*-values (two-sided Wilcoxon ranksum test) and effect sizes for the difference in timescales between neurons selective to task-relevant signals and those not selective to task-relevant signals in a given cortical area, and all areas combined. There was no significant difference between estimated timescales of the two types of neurons ($P > \frac{0.05}{20} = 0.0025$).

Timescales	Cortical area	*p*-value	Cohen's *d*	d.f.	#reward-selective	#others
Intrinsic timescales	LIP	0.48	0.05	143.80	104	77
	dmPFC	0.35	0.08	149.82	93	75
	dlPFC	0.63	0.03	269.34	127	153
	ACC	0.88	0.01	111.33	70	62
	All	0.21	0.02	803.44	394	367
Seasonal timescales	LIP	0.92	0.02	25.75	15	16
	dmPFC	0.68	0.04	49.46	42	28
	dlPFC	0.83	0.02	52.53	25	31
	ACC	0.33	0.08	43.71	29	23
	All	0.87	0.01	249.90	111	98
Reward-memory timescales	LIP	0.57	0.05	112.34	75	64
	dmPFC	0.38	0.08	95.56	58	49
	dlPFC	0.004	0.20	128.02	96	97
	ACC	0.99	0.0002	100.93	62	47
	All	0.22	0.05	556.72	291	257
Choice-memory timescales	LIP	0.94	0.006	94.50	71	53
	dmPFC	0.54	0.06	47.31	66	45
	dlPFC	0.32	0.07	121.31	78	102
	ACC	0.07	0.23	20.08	35	27
	All	0.04	0.09	409.71	250	227

Table S3. Comparisons of timescales between neurons with selectivity to reward and those with other types of selectivity. Reported are *p*-values (two-sided Wilcoxon ranksum test) and effect sizes for the difference in estimated timescales between reward and non-reward selective (i.e., those selective to choice or interaction of reward and choice) neurons, separately for each cortical area and across all areas. There was no significant difference between neurons selective to reward and the non-reward signals in a given area or across all areas ($P > \frac{0.05}{20} = 0.0025$).

Timescales	Cortical area	*p*-value	Cohen's *d*	d.f.	#choice-selective	#others
Intrinsic timescales	LIP	0.36	0.07	148.25	106	75
	dmPFC	0.02	0.17	119.82	105	63
	dlPFC	0.42	0.05	266.59	146	134
	ACC	0.05	0.15	43.89	28	104
	All	0.07	0.12	800.19	385	376
Seasonal timescales	LIP	0.73	0.04	28.81	18	13
	dmPFC	0.66	0.05	44.50	43	27
	dlPFC	0.85	0.02	55.31	29	27
	ACC	0.40	0.12	4.83	5	47
	All	0.30	0.06	254.68	95	114
Reward-memory timescales	LIP	0.54	0.05	104.27	81	58
	dmPFC	0.96	0.005	80.48	64	43
	dlPFC	0.02	0.17	160.20	106	87
	ACC	0.69	0.04	24.37	21	88
	All	0.0007	0.14	464.38	272	276
Choice-memory timescales	LIP	0.27	0.10	83.44	68	56
	dmPFC	0.19	0.12	38.62	73	38
	dlPFC	0.46	0.05	92.22	98	82
	ACC	0.93	0.01	57.25	12	50
	All	0.21	0.05	409.97	251	226

Table S4. Comparisons of timescales between neurons with selectivity to choice and those with other types of selectivity. Reported are *p*-values (two-sided Wilcoxon ranksum test) and effect sizes for the difference in estimated timescales between choice and non-choice selective (i.e., those selective to reward or interaction of reward and choice) neurons, separately for each cortical area and across all areas. Orange shading indicates a significant effect. There was only a significant difference between reward-memory timescales for neurons selective to choice and the non-choice signals across all areas ($P < \frac{0.05}{20} = 0.0025$).

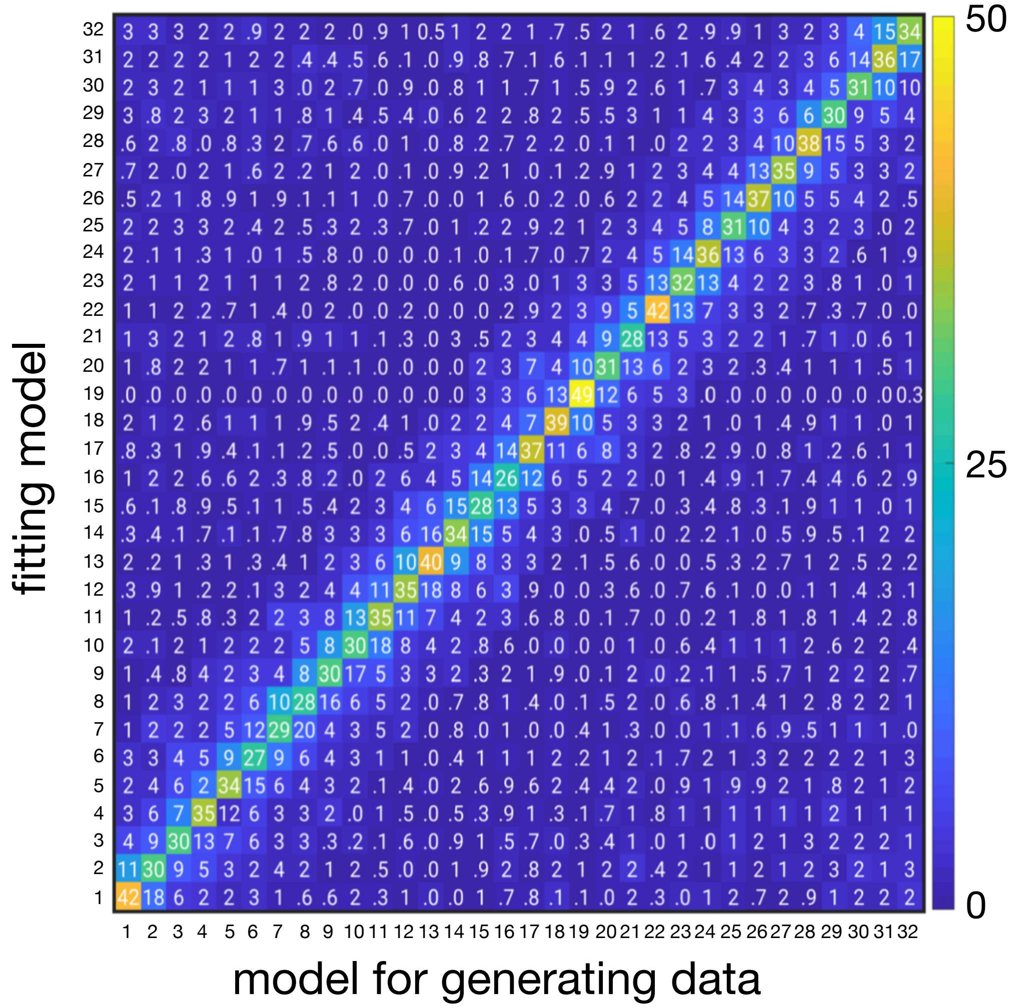

Figure S1. Model recovery. Our method is able to identify the correct model. The value of each cell reports the percentage of instances that a model used to generate the data (shown on the x-axis) was best fit by another model (fitting model, shown on the y-axis). The model corresponding to each number is provided in **SI Appendix, Table S1**. The model with the minimum AIC was assigned as the best model. The probability for assigning the best model by chance is ~3% and thus, values above 25% on the diagonal indicate that in most cases the correct model was identified. For these simulations, we generated 5000 sets of simulated neural data based on a given model and activity profile of recorded neurons, and then fit those data with all the models in order to calculate the AIC and determine the best model.

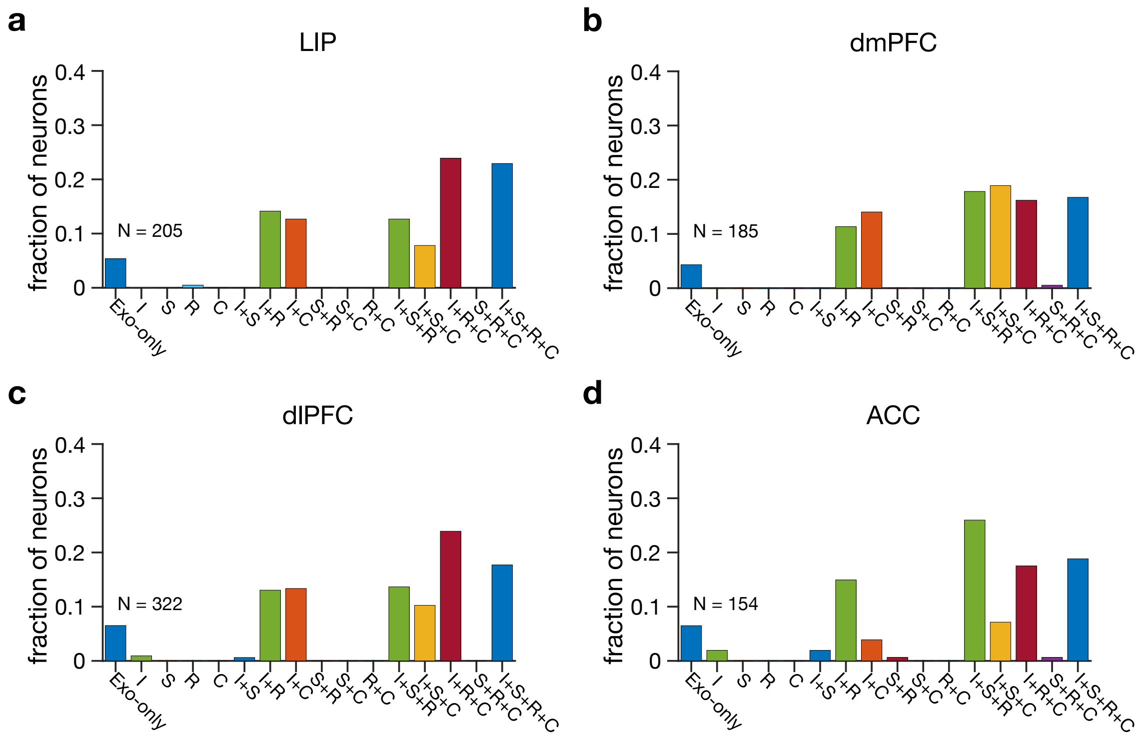

Figure S2. Response of most neurons was best captured using the model with three or more AR or memory components (component with associated timescales). Plots show the fractions of neurons whose activity was best fit by a given model, separately in each of the four cortical areas. Different types of models include: Exo-only, models with only exogenous component and no timescale; I, models with intrinsic timescale; S, models with seasonal timescale; R, models with reward-memory timescale; and C, models with choice-memory timescale. Overall, the models with three or more timescales were able to capture the response of most neurons in all cortical areas (LIP: $fraction_{\geq 3} = 0.67, \chi^2 = 15.42, p = 5.46 \times 10^{-5}$; dmPFC: $fraction_{\geq 3} = 0.70, \chi^2 = 21.85, p = 3.98 \times 10^{-6}$; dlPFC: $fraction_{\geq 3} = 0.66, \chi^2 = 10.32, p = 4.28 \times 10^{-4}$; ACC: $fraction_{\geq 3} = 0.70, \chi^2 = 12.70, p = 7.37 \times 10^{-4}$).

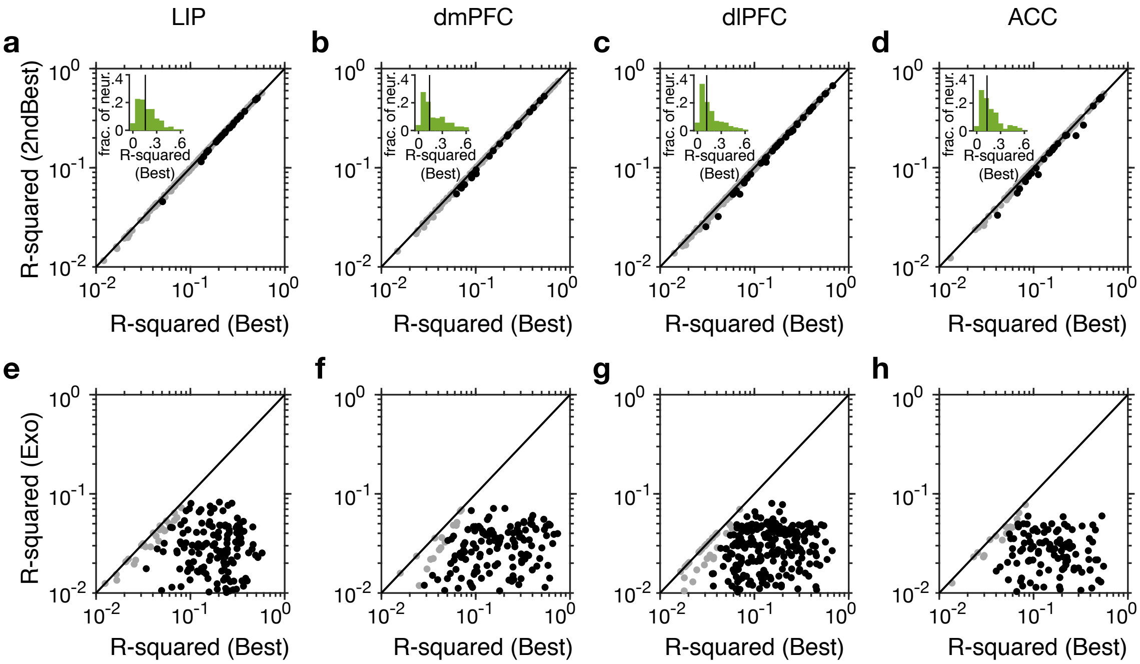

Figure S3. Best model for individual neurons can predict neural response significantly better than the second-best models and models with exogenous component only. Plots show R-squared values for the second-best model vs. those of the best models (**a**–**d**) and R-squared values for the model with exogenous component only vs. those of the best models (**e**–**h**), separately for different cortical areas indicated on the top. Neurons for which the goodness-of-fit for the best model was significantly better than that of the second-based model (or the model with exogenous component only) are shown in black. The insets in the top row show the distributions of the R-squared values for the best models. By definition, R-squared values and the difference in R-squared between the best and second-best models are positive. The differences between the medians of R-squared values for the best model and the model with exogenous component only were significantly different form zero in all cortical areas (two-sided Wilcoxon ranksum test; LIP: $p = 0.002$; dmPFC: $p = 0.002$; dlPFC: $p = 0.003$; ACC: $p = 0.001$).

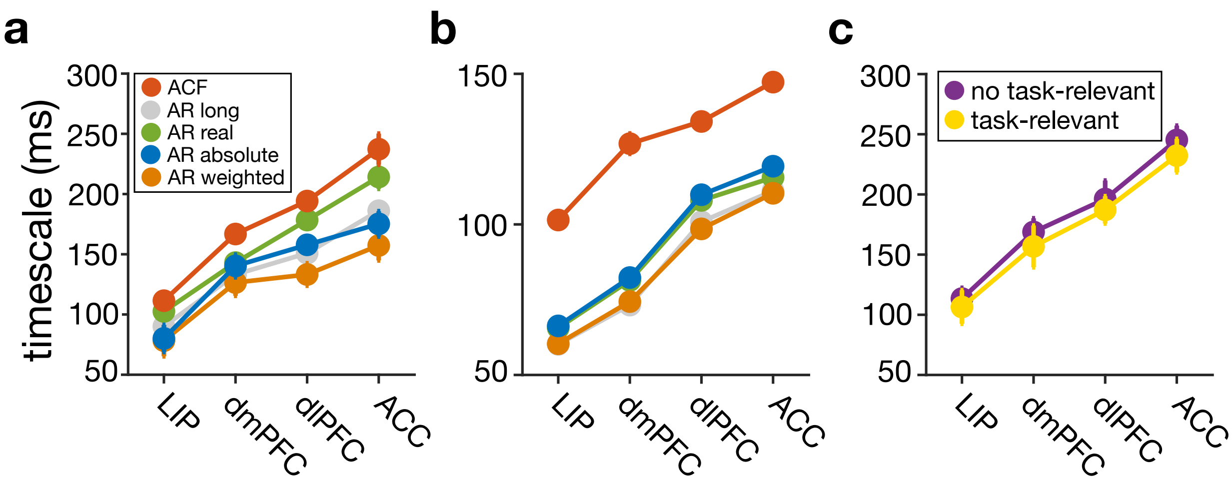

Figure S4. Comparison of the hierarchy of intrinsic timescales across cortex based on the activity during the fixation period and the entire trial estimated by different methods, and lack of evidence for the dependence of intrinsic timescales on the overall selectivity to task-relevant signals. (**a**) Plot shows the medians of the estimated intrinsic timescales in four cortical areas using autocorrelation function (ACF) during the fixation period and four different methods based on the coefficients of intrinsic AR model in the same epoch: maximum real eigenvalue (AR real), weighted average of eigenvalues (AR weighted), maximum absolute eigenvalue (AR absolute), and longest timescales based on the inverse of individual AR coefficients (AR long). Error bars indicate s.e.m. (**b**) Plot shows the medians of the estimated intrinsic timescales in four cortical areas using neural response from the entire trial and different methods. Conventions are the same as in panel a. (**c**) No evidence for the dependence of intrinsic timescales on the overall selectivity to task-relevant (reward outcome and choice) signals based on autocorrelation. Plot shows the median of the estimated intrinsic timescales based on autocorrelation of response during the fixation period, separately for neurons with (gold) and without (purple) any type of selectivity to task-relevant signals. There was no significant difference between intrinsic timescales of neurons with and without any task-relevant signals.

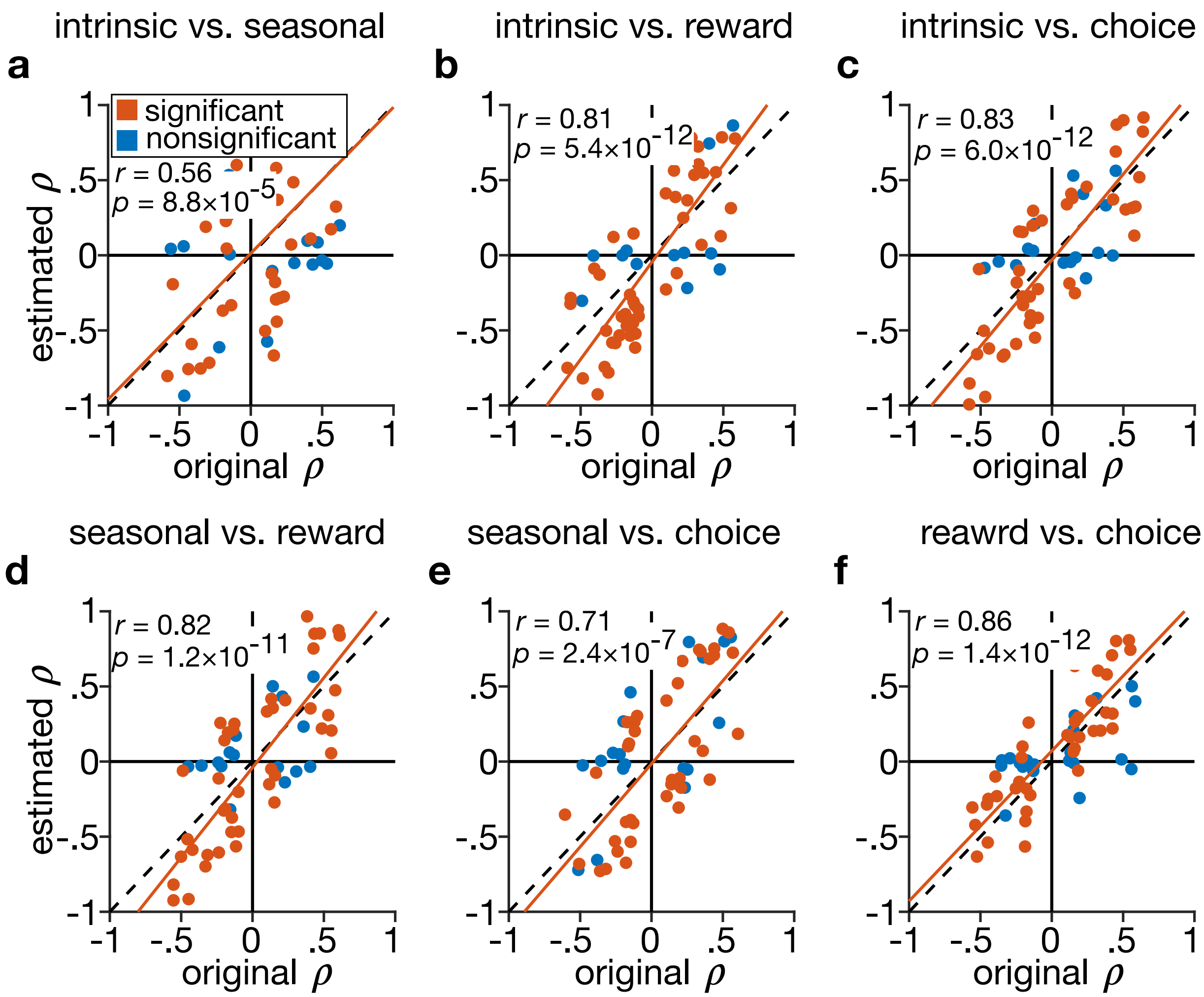

Figure S5. Our method can recover existing correlations between pairs of timescales without any systematic bias. Plots show estimated vs actual correlations coefficients between a pair of timescales (indicated on the top) across 100 individual neurons in 60 simulated datasets ($N = 60$). Red and blue dots correspond to significant ($p < 0.05$) and non-significant estimated correlations coefficients, respectively. Note that all actual correlation coefficients are significant by design. The fractions of estimated correlations that we significant in a-f are equal to 0.69, 0.82, 0.75, 0.73, 0.70, 0.68, respectively. These results show that our model can detect correlations between timescales across individual neurons within a given cortical area if such correlations exist.

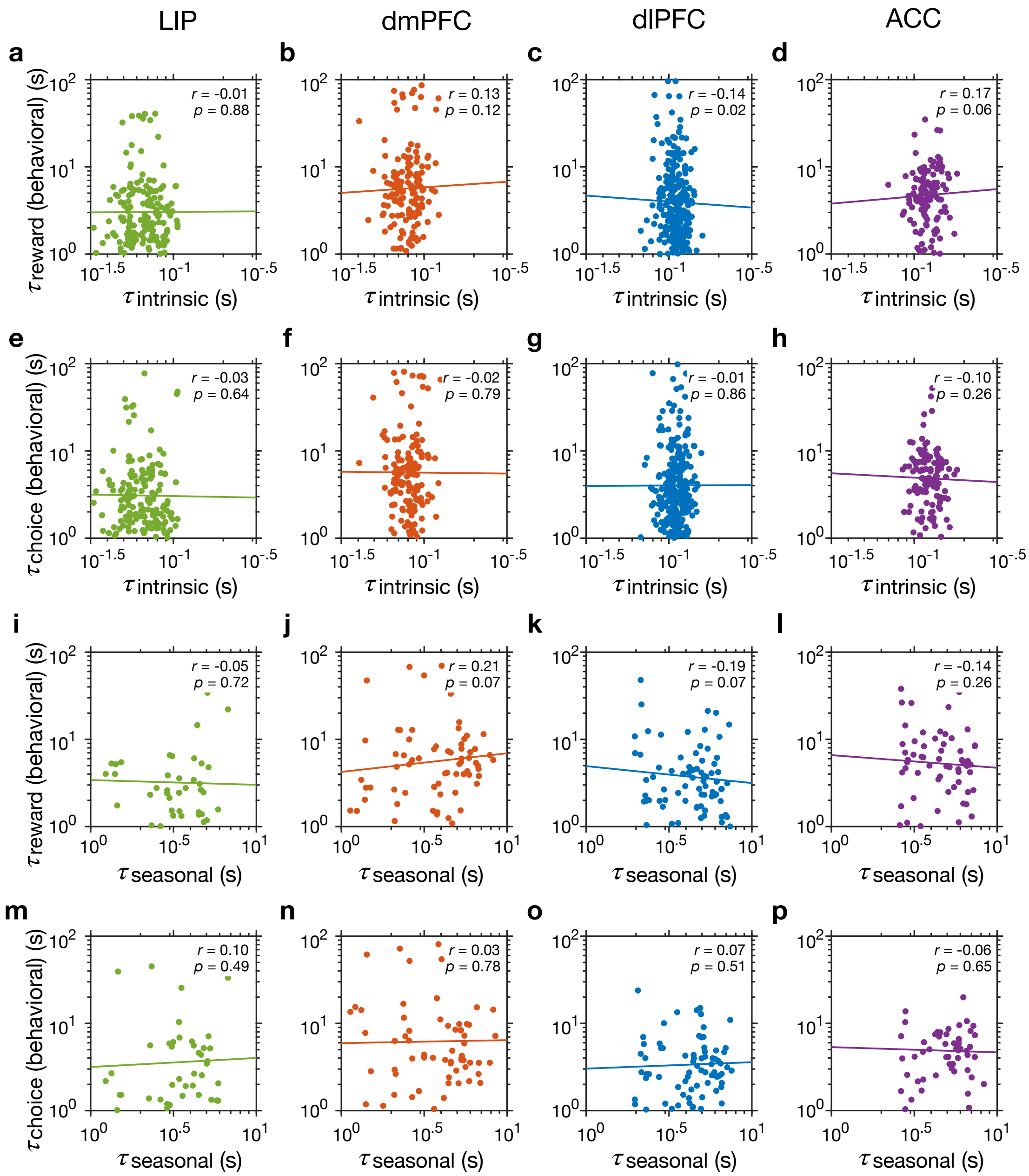

Figure S6. Lack of relationship between the two behavioral timescales and intrinsic and seasonal timescales. (**a–d**) Plots show behavioral reward timescales vs intrinsic timescales of individual neurons recorded during the same sessions, separately for different cortical areas as indicated on the top. Reported are the Spearman correlation coefficients and corresponding p-values and the solid lines represent the regression line that was fit to log values. (**e–h**) The same as in a–d but show behavioral choice timescales vs intrinsic timescales. (**i–p**) The same as in a–h but show behavioral timescales vs seasonal timescales. There was no significant correlation between behavioral and neural timescales in any cortical area ($P > \frac{0.05}{8} = 0.00625$).

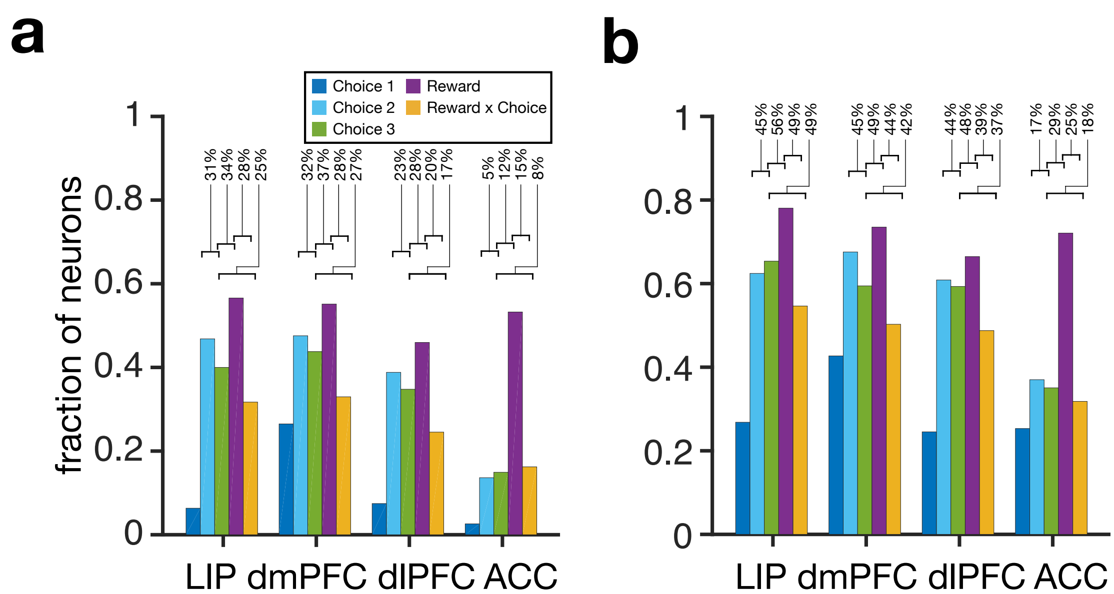

Figure S7. Similar fractions of neurons encode reward outcome across the four cortical areas, whereas the fraction of neurons selective to choice decreases from LIP to ACC. (**a**) Fraction of neurons with selectivity to reward outcome and to choice (in different epochs of the task as indicated in the legend) across the four cortical areas, estimated using the best model for individual neurons. Values on the top indicate the percentage of neurons that exhibit a combination of selectivity in a given area. Overall, about half of neurons in all cortical areas encode reward outcome with no evidence for change in the fraction of reward-selective neurons across cortex ($\chi^2(3) = 3.49, p = 0.062$). In contrast, fraction of neurons with choice selectivity decreases from LIP to ACC ($\chi^2(3) = 23.6, p = 1.2 \times 10^{-6}$ for Choice 3). ACC exhibited the smallest fraction of choice-selective neurons (LIP vs. ACC, $p = 1.3 \times 10^{-5}$; dmPFC vs. ACC, $p = 1.8 \times 10^{-6}$; dlPFC vs. ACC, $p = 1.4 \times 10^{-4}$). (**b**) The same as in panel a but using the model that only includes the exogenous term and no timescales.

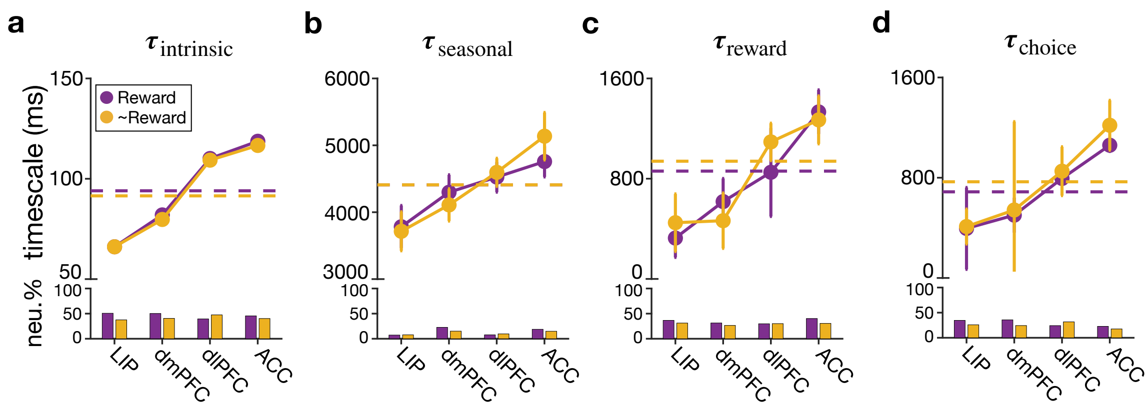

Figure S8. Independence between timescales and the selectivity to reward vs. other task-relevant (choice and interaction of choice and reward) signals. Plots show the median of the estimated intrinsic (**a**), seasonal (**b**), reward-memory (**c**), and choice-memory **(d)** timescales in four cortical areas, separately for neurons selective to reward outcome (purple) and neurons not selective to reward outcome (i.e., those selective to choice or interaction of reward and choice; gold). The dashed lines show the median across all four areas. Error bars indicate s.e.m., and asterisks mark a significant difference between the medians of two types of neurons in a given area or across all areas (two-sided Wilcoxon ranksum test, $P < \frac{0.05}{20} = 0.0025$; see **SI Appendix, Table S3** for detailed statistics). Bar graphs show the fractions of neurons selective to reward and neurons selective to non-reward signals in each area. In this analysis, we only included neurons that exhibited selectivity to task-relevant signals.

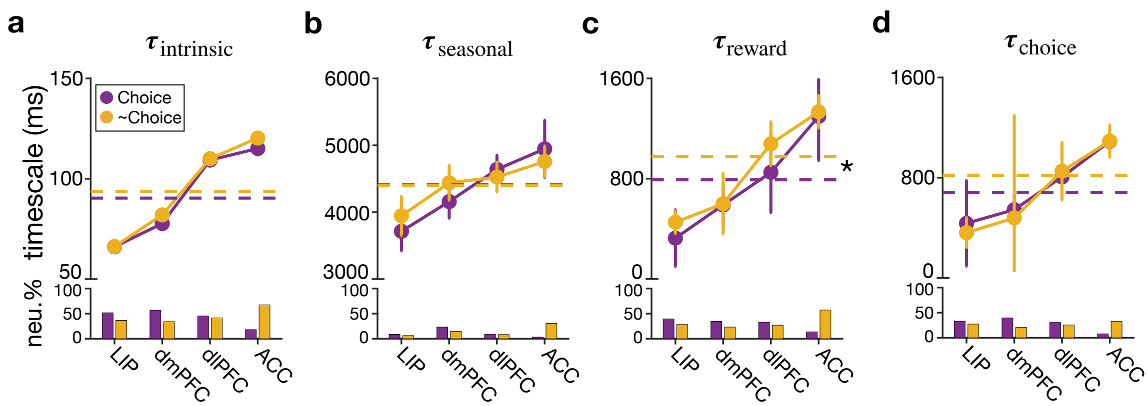

Figure S9. Relationship between timescales and the selectivity to choice vs. other task-relevant (reward and interaction of choice and reward) signals. Plots show the median of the estimated intrinsic (**a**), seasonal (**b**), reward-memory (**c**), and choice-memory (**d**) timescales in four cortical areas, separately for neurons selective to choice (purple) and neurons not selective to choice (i.e., those selective to reward or interaction of reward and choice; gold). The dashed lines show the median across all four areas. Error bars indicate s.e.m., and asterisks mark a significant difference between the medians of two types of neurons in a given area or across all areas (two-sided Wilcoxon ranksum test, $P < \frac{0.05}{20} = 0.0025$; see **SI Appendix, Table S4** for detailed statistics). Bar graphs show the fractions of neurons selective to choice and neurons selective to non-choice signals in each area. In this analysis, we only included neurons that exhibited selectivity to task-relevant signals.

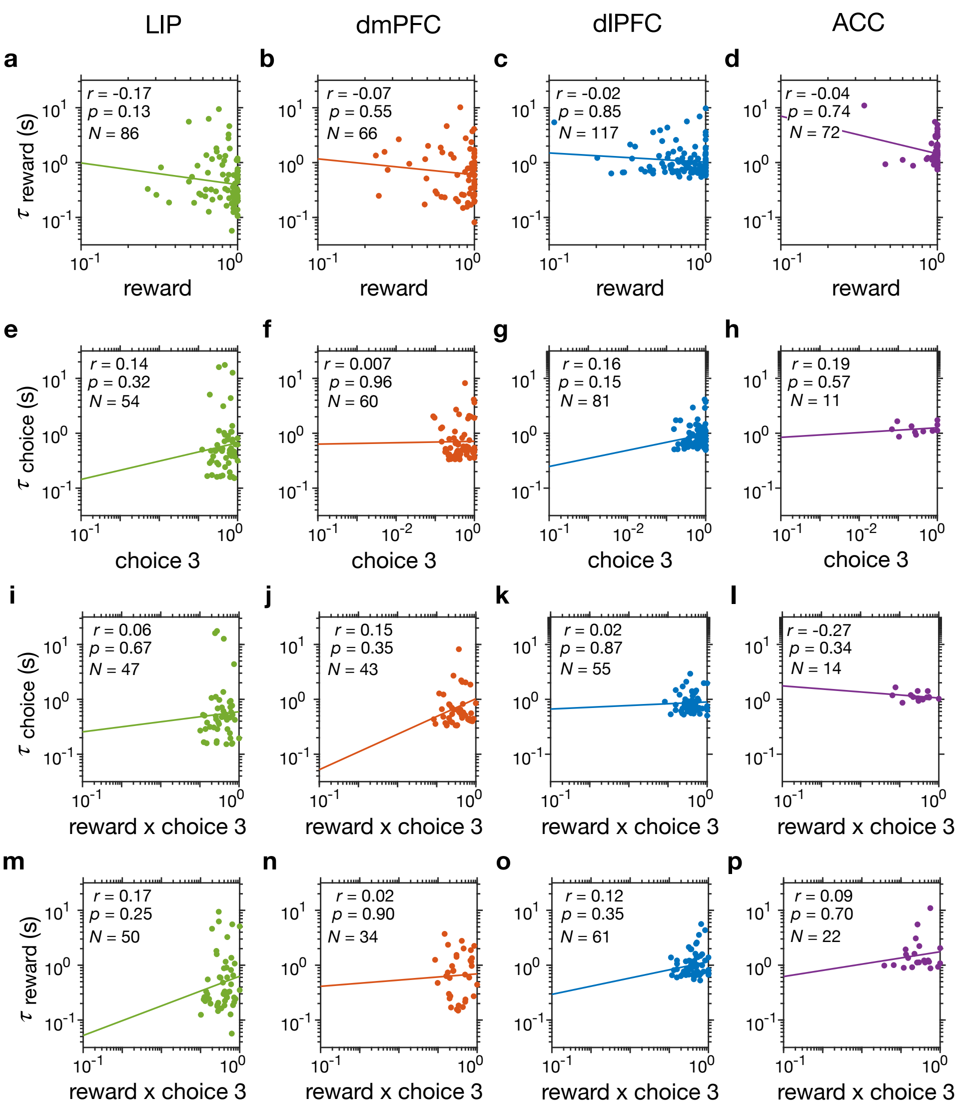

Figure S10. Independence between different types of choice- and reward-memory timescales and magnitudes of response to different task-relevant signals. (**a–d**) Plots show the estimated reward-memory timescales vs. absolute standardized magnitude of reward regressor (as a measure of the selectivity strength) within individual neurons, separately for different cortical areas indicated on the top. Reported are the Spearman correlation coefficients and corresponding *p*-values, and the number of neurons with a significant value of a given timescale. The solid lines represent the regression line that was fit to log values. (**e–h**) The same as in **a–d** but plotting the estimated choice-memory timescales vs. absolute standardized magnitude of choice regressor. (**i–p**) Plots show the estimated choice- (**i–l**) and reward-memory (**m–p**) timescales vs. absolute standardized magnitude of interaction between reward and choice regressors within individual neurons. There was no significant correlation between corresponding memory timescales and exogenous signal magnitude in any of the cortical areas ($P > \frac{0.05}{16} = 0.0031$).

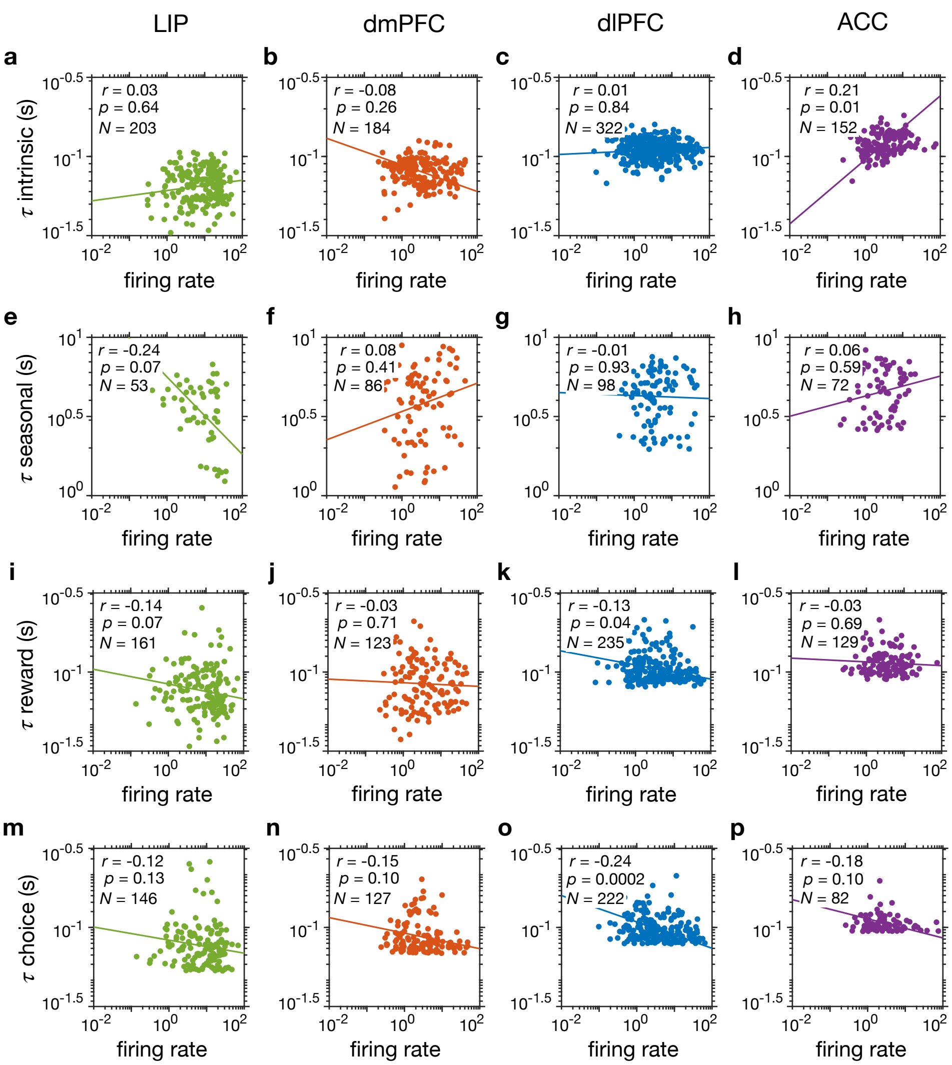

Figure S11. Independence between different types of timescales and firing rates within individual neurons. Panels show scatterplots of estimated intrinsic (**a-d**), seasonal (**e-h**), reward- (**i-l**), and choice- (**m-p**) memory timescales vs. mean firing rates of individual neurons, separately for different cortical areas indicated on the top. Reported are the Spearman correlation coefficients and corresponding *p*-values, and the number of neurons with a significant value of a given timescale. The solid lines represent the regression line that was fit to log values. There was no significant correlation between timescales and firing rates in any of the cortical area ($P > \frac{0.05}{16} = 0.0031$) except for choice-memory and firing rate in the dlPFC where more active neurons showed smaller timescales.