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Figures and figure supplements

Vacillation, indecision and hesitation in moment-by-moment decoding of monkey motor cortex

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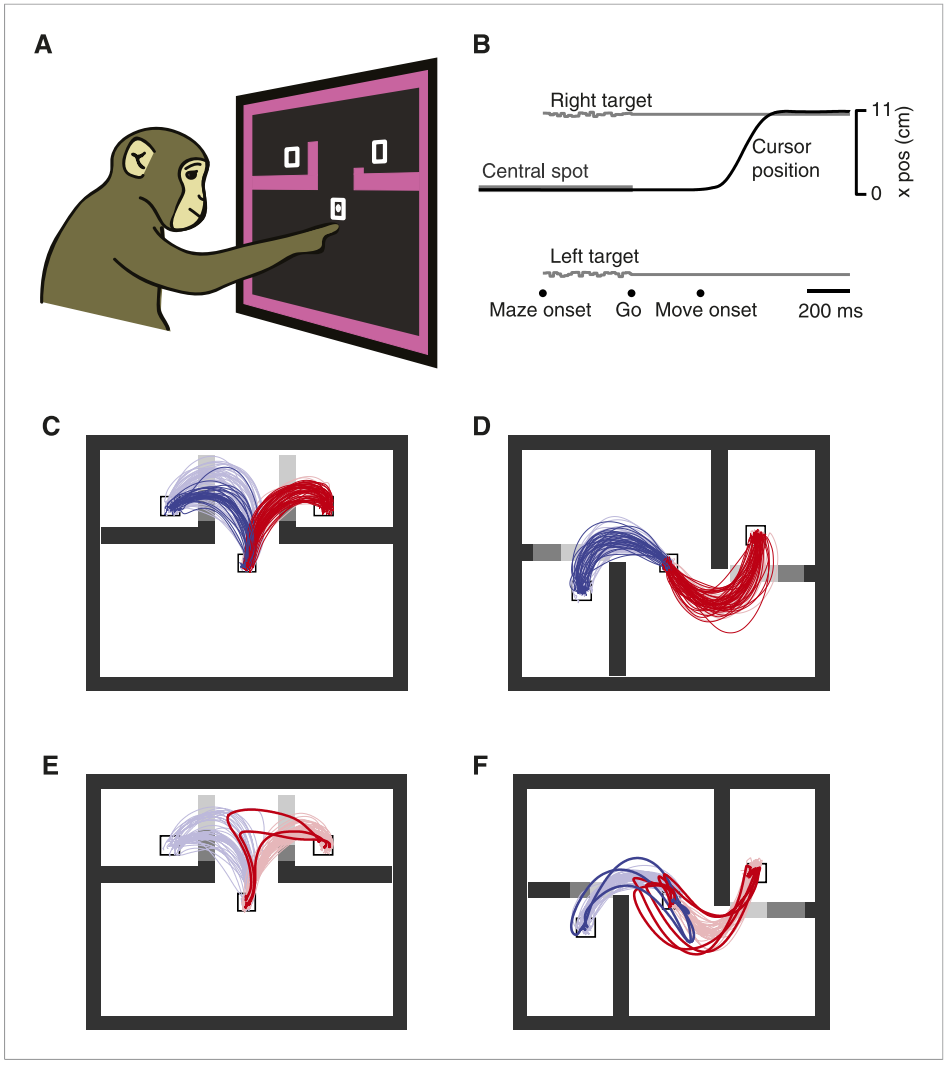

Figure 1. Decision-maze task. (**A**) Illustration of task setup. Two targets were presented along with four virtual barriers and a frame. The monkey performed the task with a cursor projected above his fingertip. Targets were rewarded equally. The cursor left a white trail on the screen. (**B**) Task timeline. (**C** and **D**) The two families of mazes used: 'T-maze' (**C**) and 'S-maze' (**D**). Key barriers could take one of three positions, making each target easy, difficult, or blocked (shown here as shades of gray). Reaches for trials with ≥300 ms delay shown. Faded colors, reach trajectories on forced choice trials; saturated colors, reach trajectories on free choice trials. (**E** and **F**) Overt changes of mind on free-choice trials with no barrier changes. Dataset J1 (**A**–**E**); dataset N3 (**F**).

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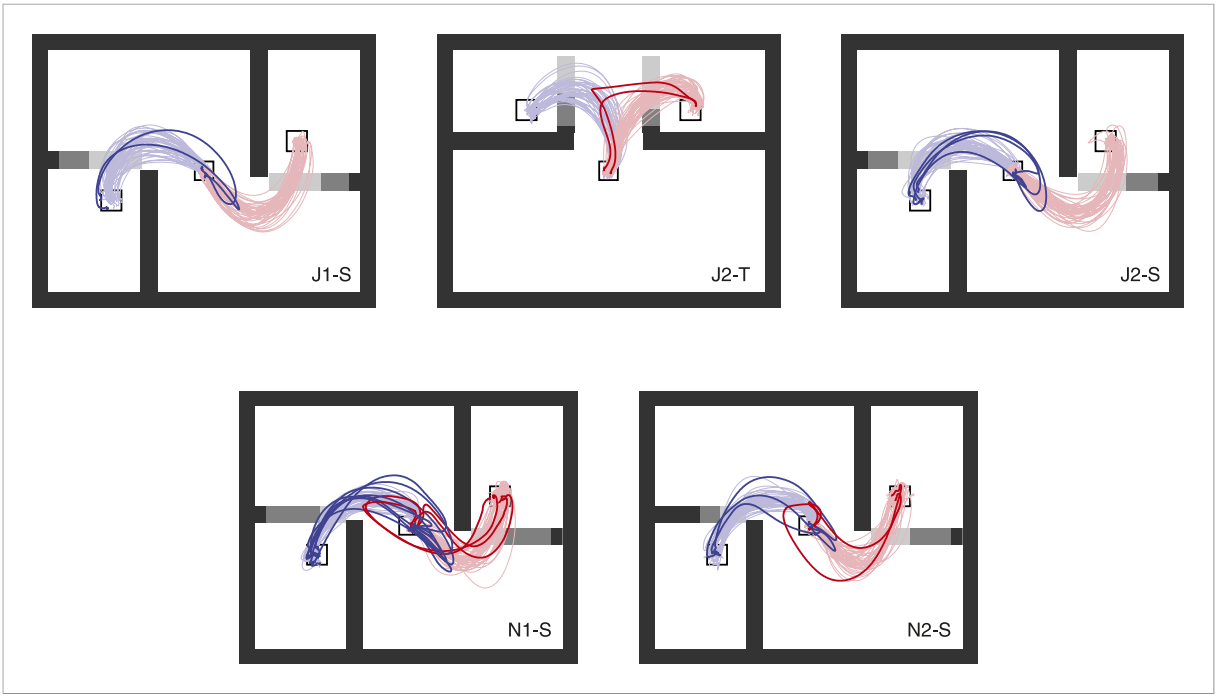

Figure 1—figure supplement 1. Overt changes of mind for the other five datasets (labeled on panels). Displayed as in ***Figure 1E,F***.
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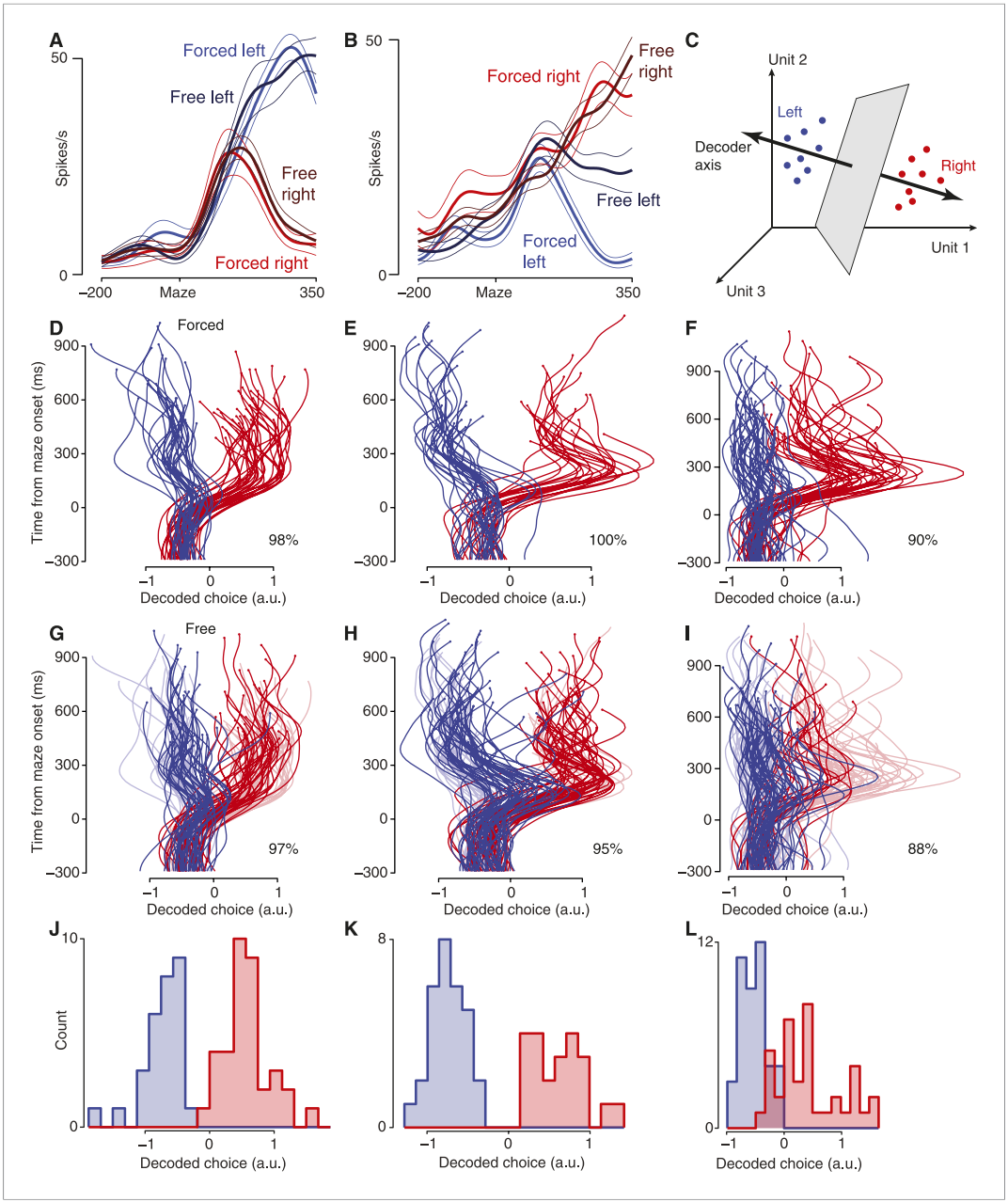

Figure 2. Firing rates and decoding. Blue represents eventual leftward reaches, red indicates eventual rightward reaches. (**A** and **B**) Responses of example units, dataset J2-S. Thick traces, mean; thin traces, s.e.m, Maze, maze onset. Time in ms. Selectivity for left vs right movements was common, and responses were almost always similar for forced and free reaches (**A**). Less commonly, forced and free evoked somewhat different responses (**B**). (**C**) Schematic of decoder. Each dot represents neural state in a window of time on a single trial. (**D**–**F**) Decoded choice plots for forced-choice trials, generated by leave-one-out cross-validation. Percentages show fraction correct classification. Datasets J2-T (**D**), J2-S (**E**), N1-S (**F**). Small dots are at last decoded time point. (**G**–**I**) Decoded choice plots for free-choice trials (saturated colors) with forced-choice trials shown for context (faded colors). Datasets same as **D**–**F**. (**J**–**L**) Cross-validated decoded choice at final point for forced-choice trials. Datasets same as **D**–**F**.

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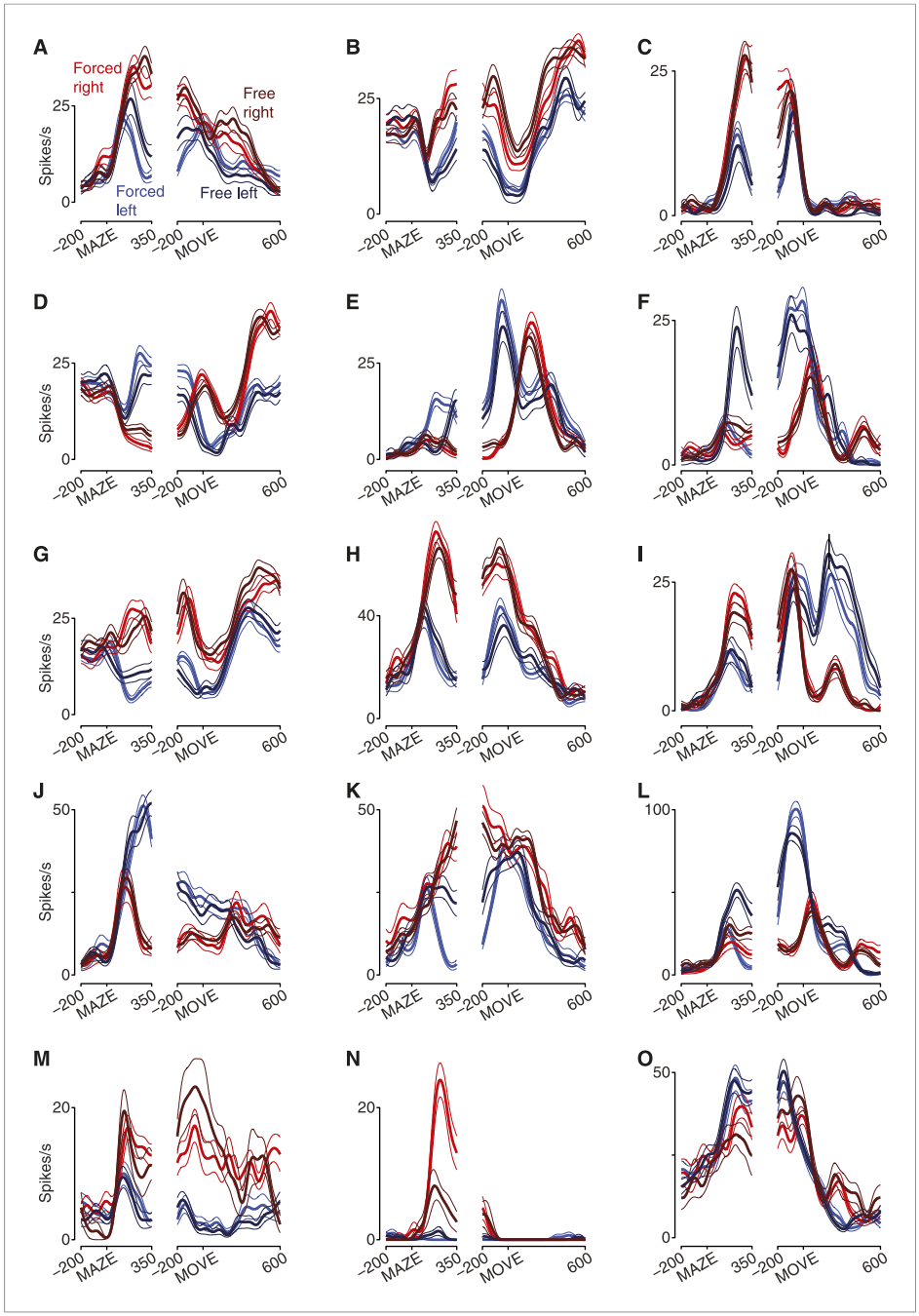

Figure 2—figure supplement 1. PSTHs for more example units. Both the preparatory epoch and the peri-movement epoch are shown. For display, we selected units that attained different firing rates for right vs left during preparation and which reflected the diversity of responses observed. (**A**–**C**) Units from J1-T. (**D**–**F**) Units from J1-S. (**G**–**I**) Units from J2-T. (**J**–**L**) Units from J2-S. (**M**–**O**) Units from N1-S. Units shown in panels **J** and **K** are the same units from ***Figure 2A,B***. MAZE, target/maze onset; MOVE, movement onset.

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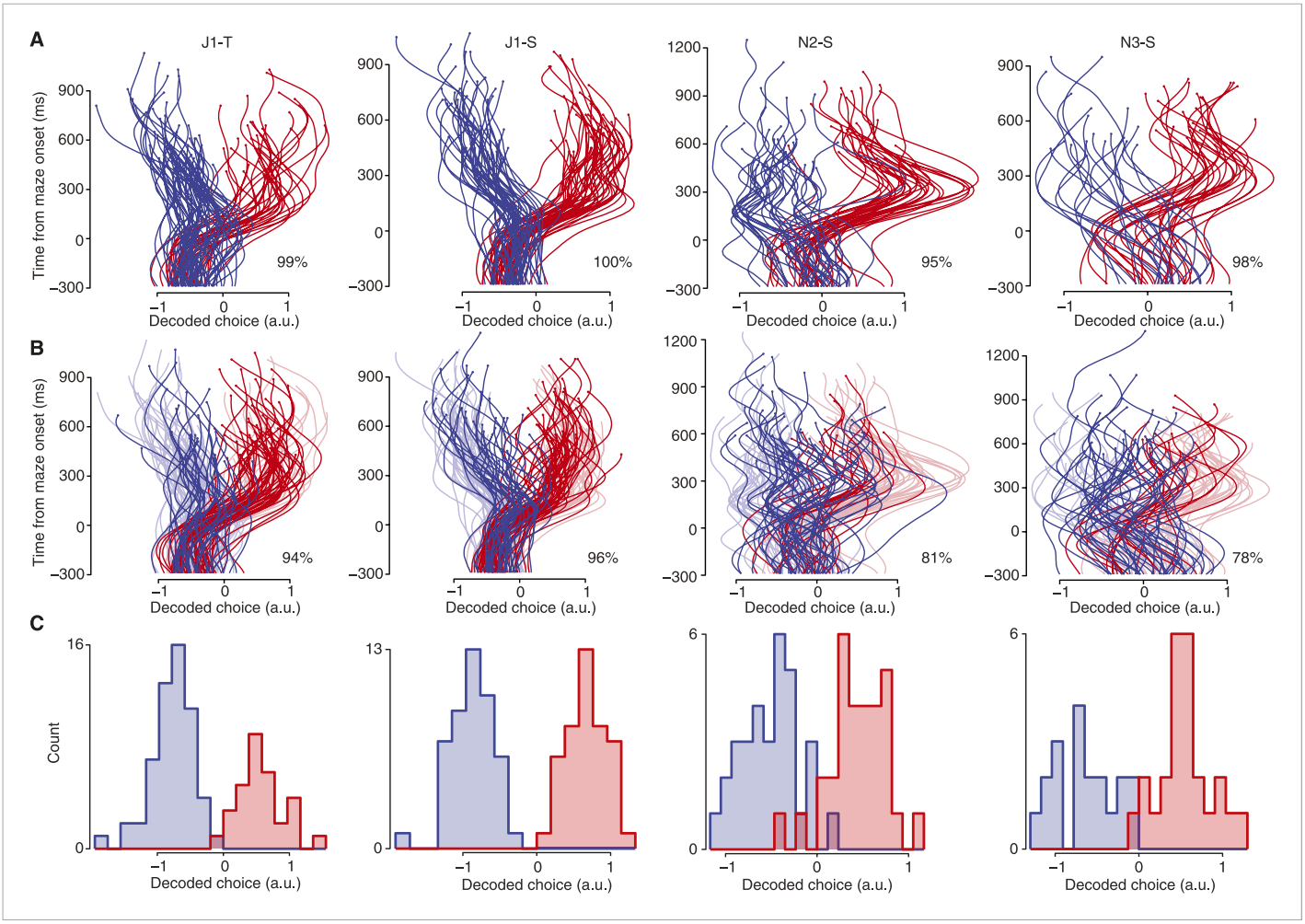

Figure 2—figure supplement 2. Decoding forced and free choices. These plots are like ***Figure 2D–I***, for the remaining datasets. (**A**) Cross-validated decoded choices for forced-choice trials. Column headers indicate dataset. (**B**) Decoded choices for free choice trials using the decoder trained on forced-choice trials (saturated colors). Forced-choice trials shown in faded colors for context. (**C**) Cross-validated decoded choices at final point for forced-choice trials.

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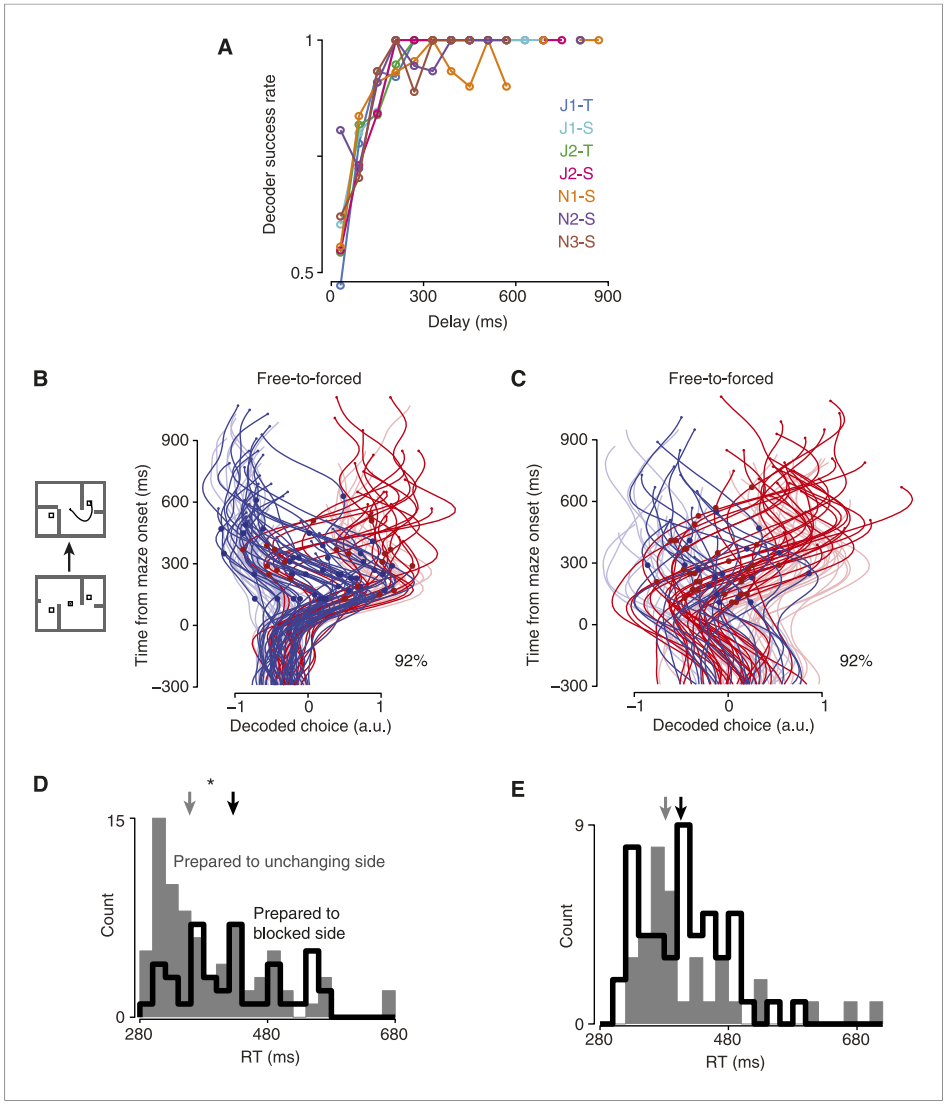

Figure 3. Validating the decoder. (**A**) Decoder performance vs time, forced-choice trials. (**B**) Maze icons illustrate free-to-forced trials. Saturated colors show the decoded choice for free-to-forced trials, which began as free but became forced when a barrier changed during the delay epoch. Faded colors show forced-choice trials for context. Large red dots indicate time of changes that made the rightward target the only available option; blue dots, leftward. Percentage indicates the fraction of trials for which the final decoded time point matched the monkey's choice. Dataset J2-S. (**C**) Same for dataset N3-S. (**D**) RT distributions for free-to-forced trials in which the barrier changed around the time of the Go cue. Black, trials where the monkey initially prepared a reach to the now-blocked side; gray, to the unchanging side. Data for monkey J pooled. Arrows, medians. (**E**) Same for monkey N.

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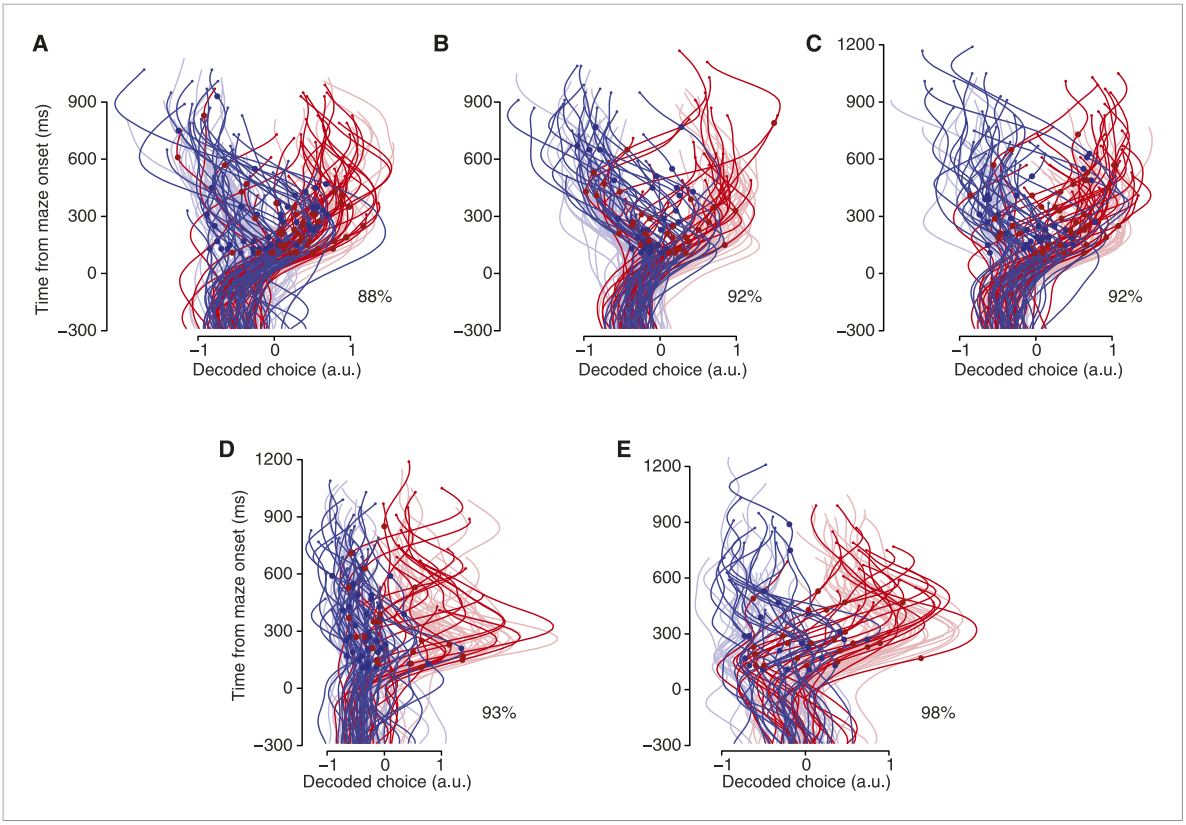

Figure 3—figure supplement 1. Decoded choices for free-to-forced trials. These plots are like ***Figure 3B,C***, for the remaining datasets. (**A**) J1-T. (**B**) J1-S. (**C**) J2-T. (**D**) N1-S. (**E**) N2-S.

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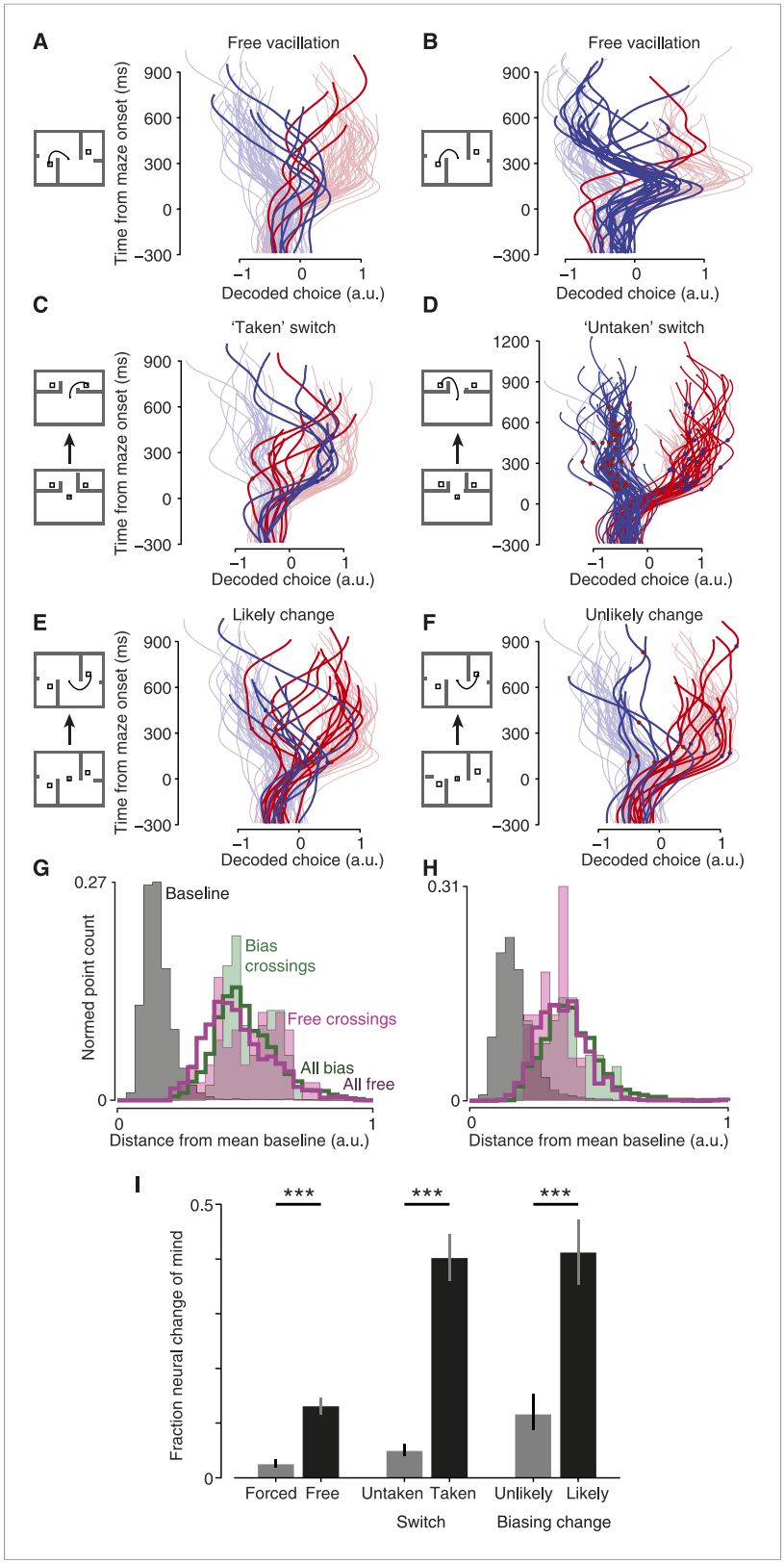

Figure 4. Covert changes of mind. Maze icons indicate situation for adjacent decoded choice plots (saturated colors), with faded colors showing forced-choice trials for context. (**A** and **B**) Apparent 'vacillation' on free choice trials. Datasets J1-S (**A**) and J2-S (**B**). (**C** and **D**) Encouraged switch trials, which began as forced but became free when a barrier changed mid-delay. Red dots on traces indicate time of changes that made the rightward target

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Figure 4. Continued

more attractive; blue dots, leftward more attractive. J2-T. (**C**) Trials where the monkey chose the newly-available target. (**D**) Trials where the monkey chose the always-available target. (**E** and **F**) Biasing change trials. These trials were free throughout, but the difficulty of one side changed mid-delay. (**E**) Trials where the monkey reached to the target that was initially more difficult, and thus likely changed his mind. (**F**) Trials where the monkey reached to the target that was initially easier, and thus likely retained his initial decision. Dataset J1-S. (**G** and **H**) Distance from mean 'baseline state' (−300 to −40 ms from maze onset) for different trials and time epochs: during baseline (gray), during free-choice vacillations around the time of the change in the decoded choice (filled pink), during biasing-change trials around the time of the change in the decoded choice (filled green), during all times for free (hollow pink) or biasing-change (hollow green) trials. J2-S (**G**) and N1-S (**H**). (**I**) Probability that a trial of the given type exhibited a neural change of mind (a large change in the decoded choice during the delay period). See 'Results' for details. Forced vs free and untaken vs taken switch, $p < 10^{-9}$; unlikely vs likely change, $p < 10^{-4}$ (χ^2 2 × 2 contingency test). Error bars show Wilson binomial confidence intervals equivalent to 1 s.e.m.

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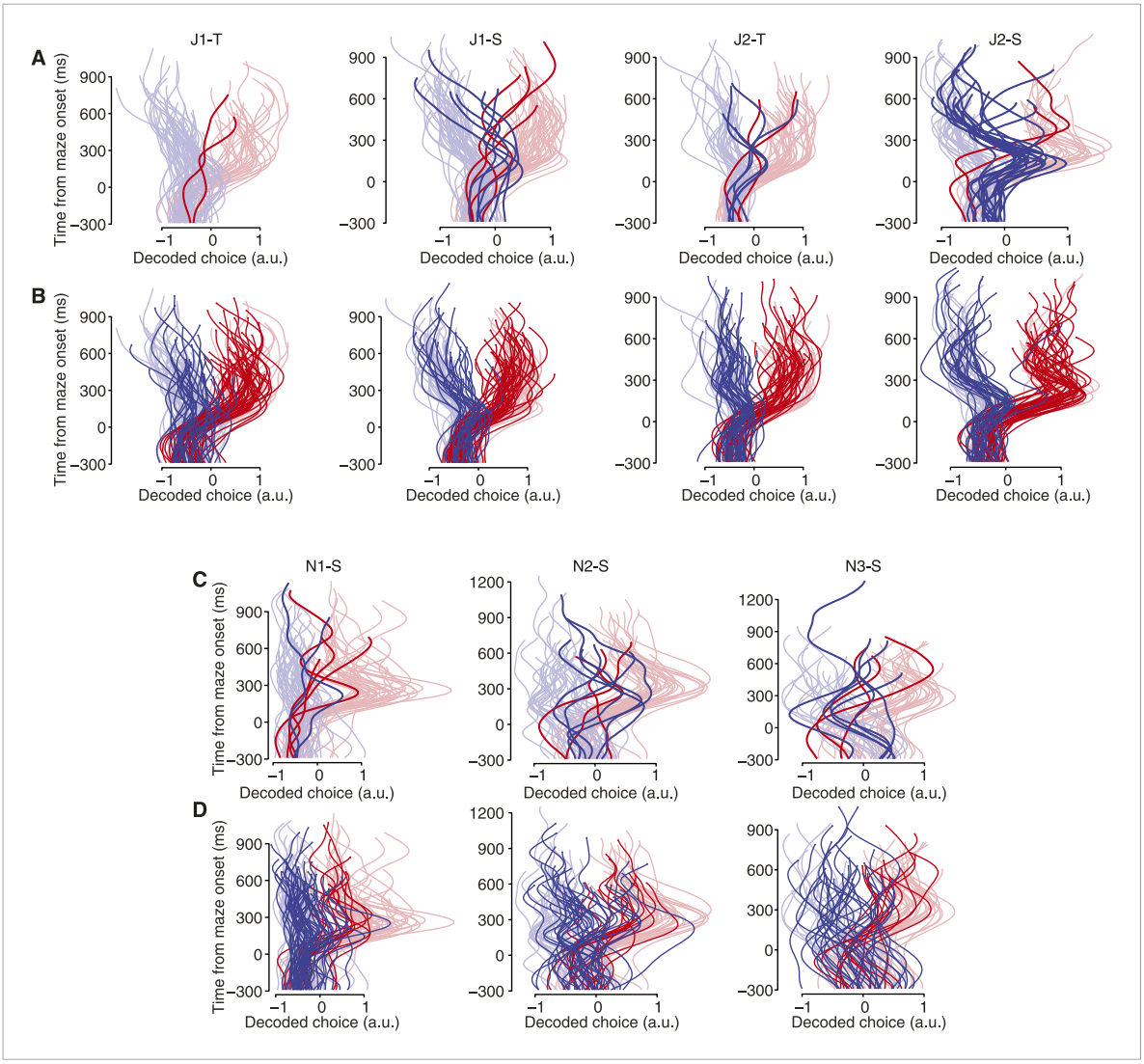

Figure 4—figure supplement 1. Free choice vacillation. All datasets contained free-choice trials exhibiting large, late changes in the decoded choice, presumably indicating spontaneous changes of mind. (**A**) Algorithmically-identified vacillation trials ('Materials and methods') shown in saturated colors; forced-choice trials shown in faded colors for context. Data from monkey J. Dataset identity indicated by column header. (**B**) All free-choice trials not included in (**A**) shown in saturated colors; faded colors same as in (**A**). (**C**) Same as (**A**) for monkey N. (**D**) Same as (**B**) for monkey N.
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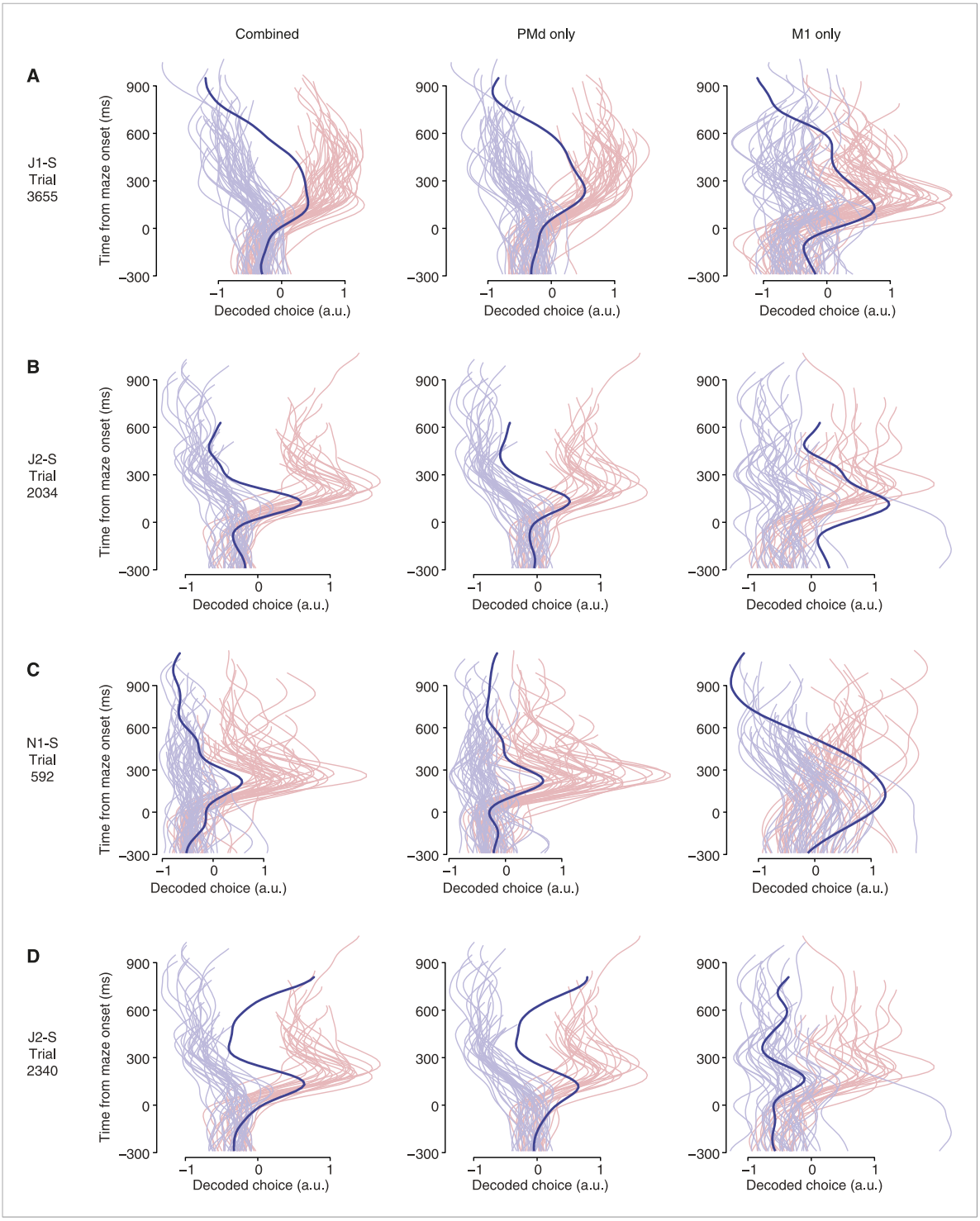

Figure 4—figure supplement 2. Example vacillation trials with choice decoded using PMd and M1 separately. Each row represents a free-choice trial (saturated-color trace) that was identified as containing a vacillation using both brain areas. Faded colors show forced-choice trials for context. The first column shows the decoded choice over time using both brain areas; the second column shows the decoded choice over time using PMd alone; the third column shows the decoded choice over time using M1 alone. (**A**–**C**) Trials in which vacillations appear similar using all three decoders. (**D**) Trial in which the M1 decoder disagreed with the combined and PMd decoders.

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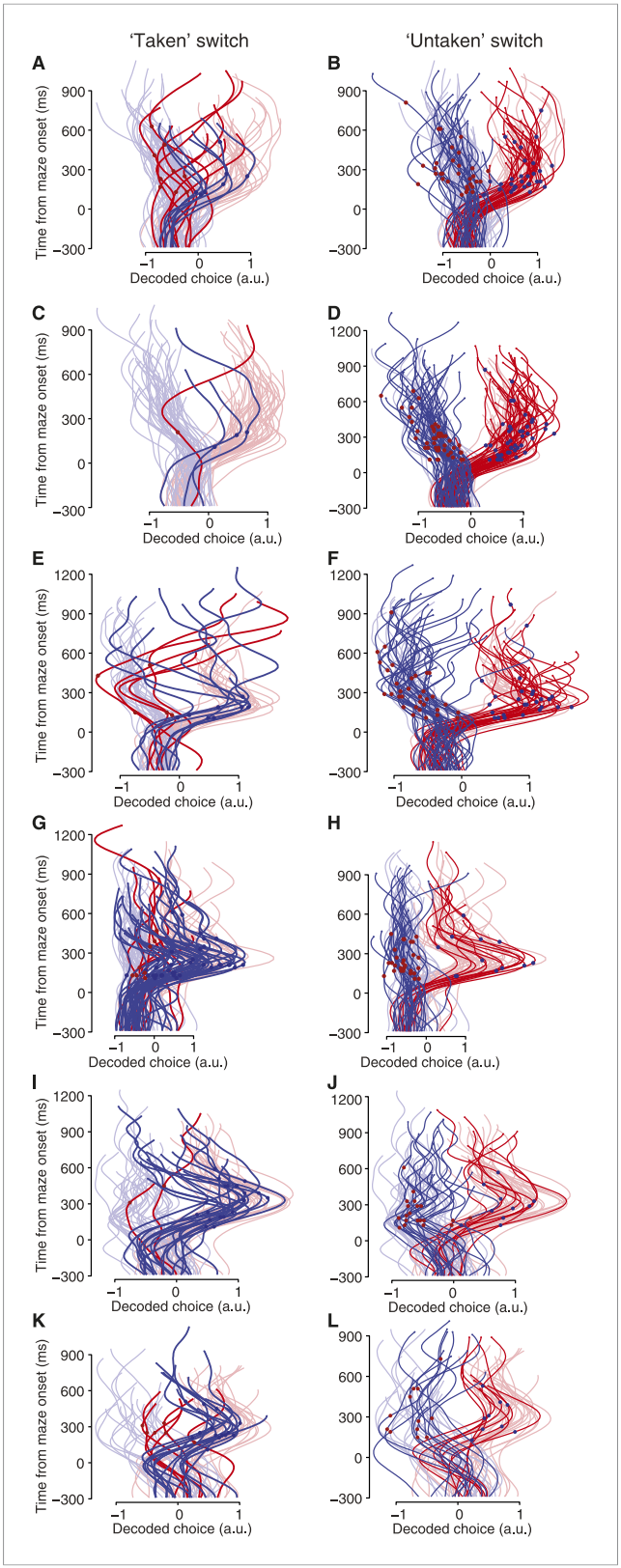

Figure 4—figure supplement 3. Decoded choices for taken switch trials (left column) and untaken switch trials (right column). These plots are like ***Figure 4C,D***, for the remaining datasets. (**A** and **B**) J1-T. (**C** and **D**) J1-S. (**E** and **F**) J2-S. (**G** and **H**) N1-S. (**I** and **J**) N2-S. (**K** and **L**) N3-S.

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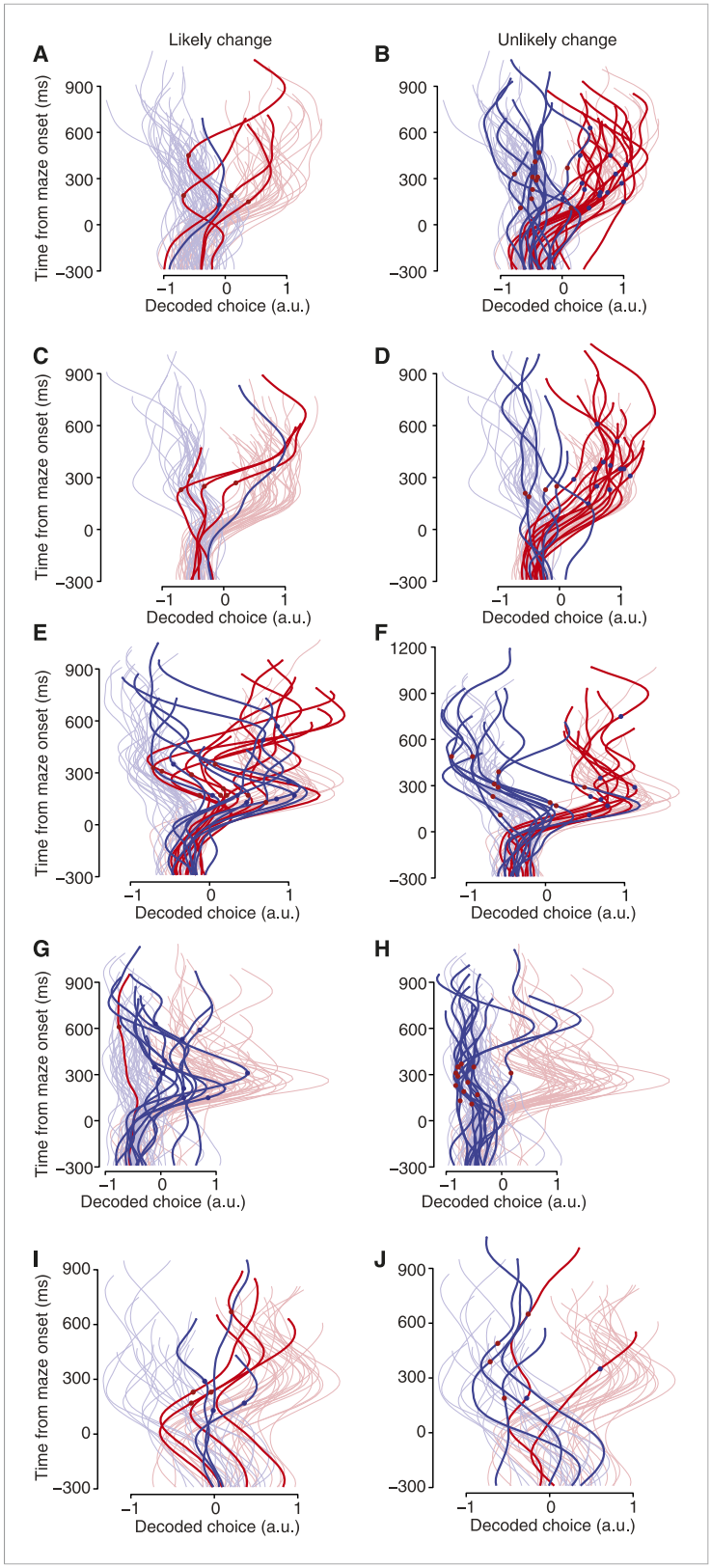

Figure 4—figure supplement 4. Biasing changes in the barriers encouraged changes of mind. These plots are like ***Figure 4E,F***, for the remaining datasets. Left column, trials where the monkey reached toward the target that was

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initially more difficult, and thus changes of mind were likely; right column, trials where changes of mind were unlikely. (**A** and **B**) J1-T. (**C** and **D**) J2-T. (**E** and **F**) J2-S. (**G** and **H**) N1-S. (**I** and **J**) N3-S.

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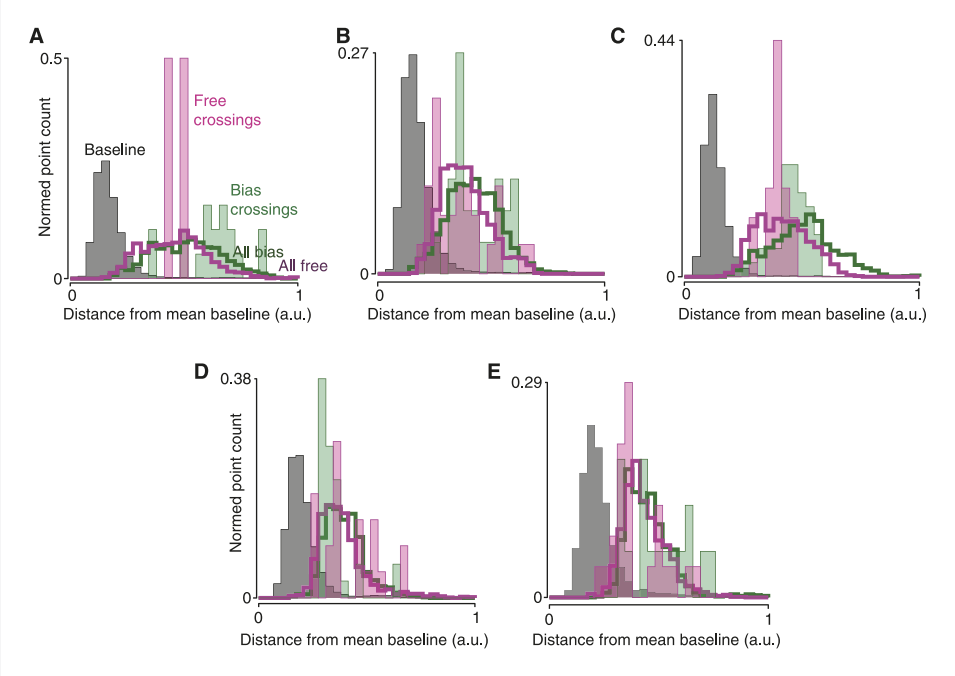

Figure 4—figure supplement 5. Neural states during changes of mind typically did not resemble the baseline state. These plots are like ***Figure 4G,H***, for the remaining datasets. (**A**) J1-T. (**B**) J1-S. (**C**) J2-T. (**D**) N2-S. (**E**) N3-S.

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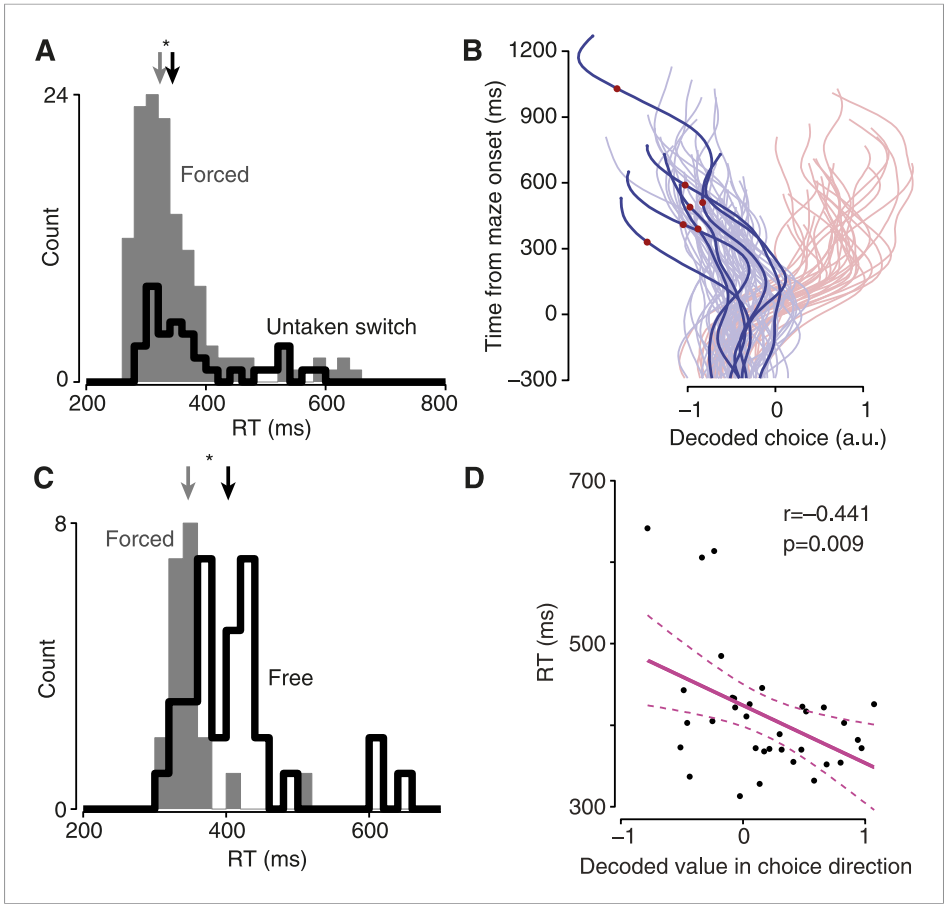

Figure 5. Hesitation and indecision. (**A**) RT distribution for forced-choice trials (gray) and encouraged switch trials in which the monkey reached to the always-available target (black). Arrows indicate medians; difference, 21 ms, p = 0.014, Mann–Whitney *U* test. Dataset J1-T. (**B**) Decoded choice for the untaken switch trials from (**A**) with RTs >450 ms (saturated colors), with forced-choice trials for context (faded colors). Red dots, time of barrier change. (**C**) RT distributions for non-delayed forced (gray) and free (black) trials. Arrows indicate medians; difference, 56 ms, p < 0.001, Mann–Whitney *U* test. Dataset J2-S. (**D**) Strength of decoded choice in direction of eventual reach (positive toward reach) at 100 ms after maze onset, vs RT for non-delayed free-choice trials. One point per trial; line indicates regression fit, dashed lines show 95% CI of fit.

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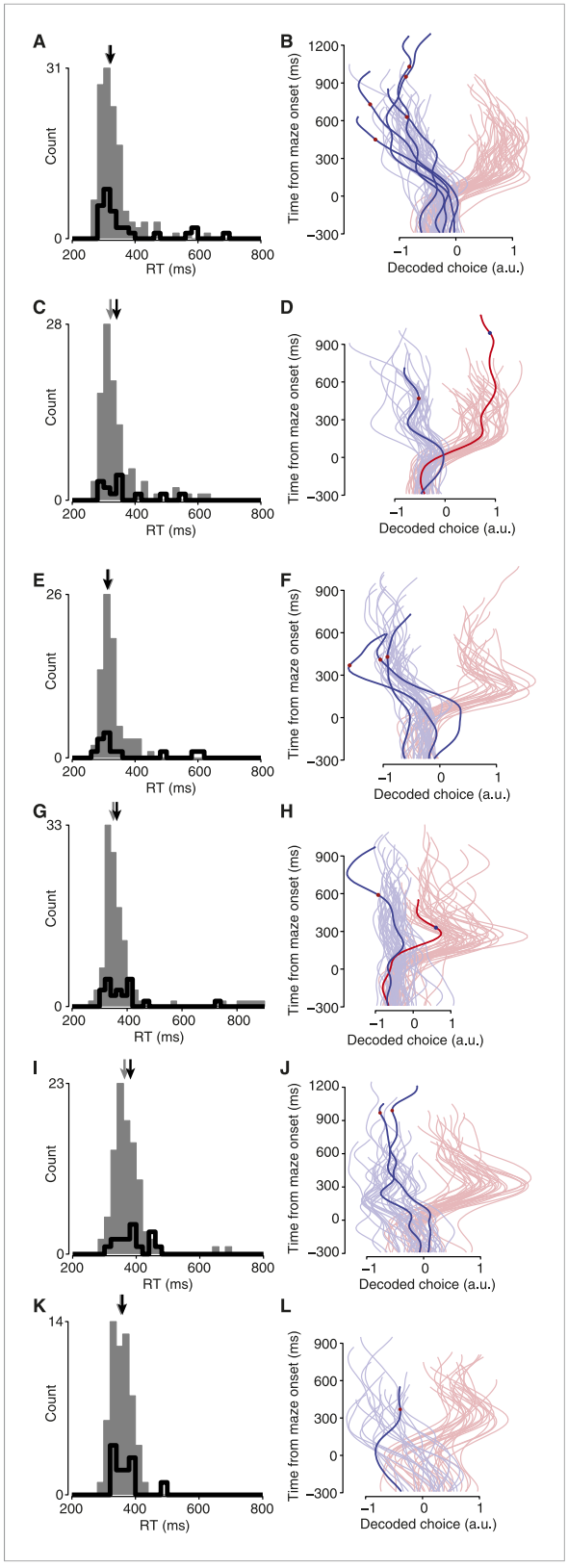

Figure 5—figure supplement 1. Decoded choice is undisturbed on slow-RT, untaken-switch trials. These plots are the same as ***Figure 5A,***

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B, for the remaining datasets. (A and B) J1-S. (C and D) J2-T. (E and F) J2-S. (G and H) N1-S. (I and J) N2-S. (K and L) N3-S.

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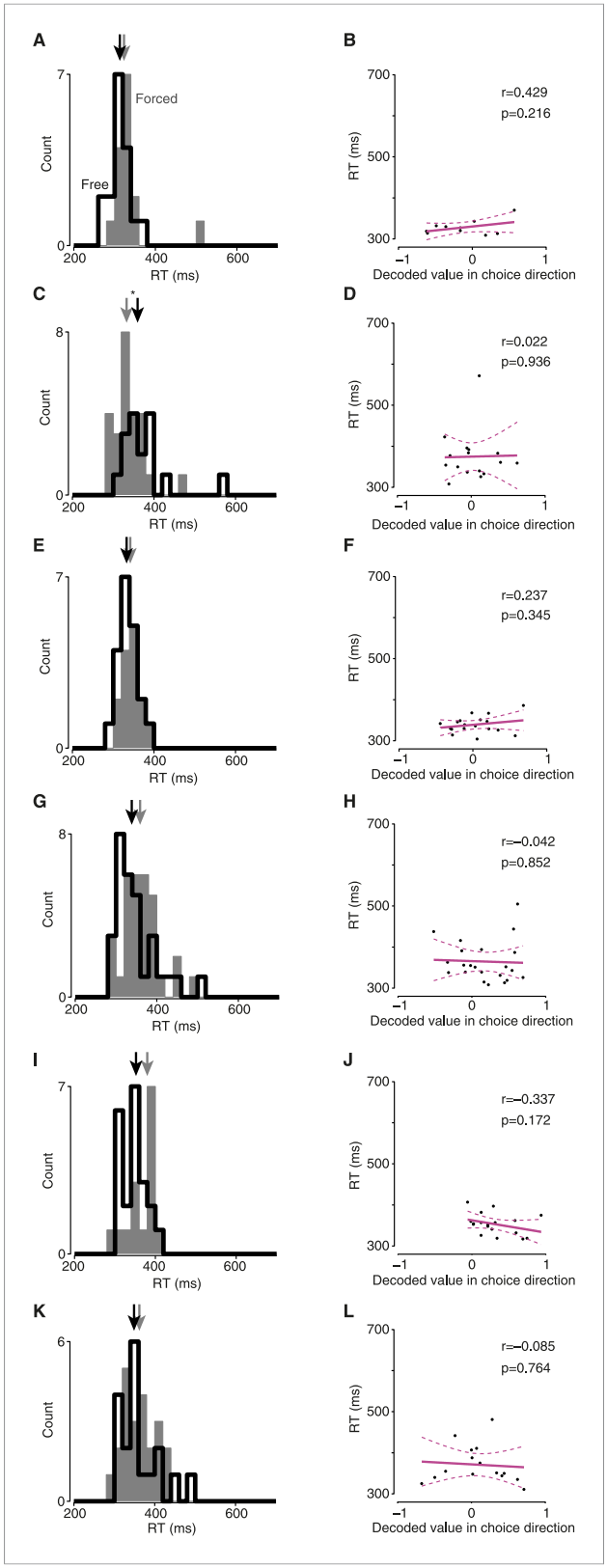

Figure 5—figure supplement 2. Slow-RT free-choice trials were rare in other datasets (J2-S shown in ***Figure 5C,D***). All trials shown had no instructed delay. Left column, RT histograms; right column, RT vs strength of decoded choice

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Figure 5—figure supplement 2. Continued

in direction of eventual reach. (**A** and **B**) J1-T. (**C** and **D**) J1-S. Free choices for this dataset were significantly slower than forced choices ($p = 0.011$), but this difference was small. (**E** and **F**) J2-T. (**G** and **H**) N1-S. (**I** and **J**) N2-S. (**K** and **L**) N3-S.

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