

Systematic changes of neural population activity during curl force field adaptation and generalization

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A hallmark of the motor system is its ability to execute different skilled movements as the situation warrants, thanks to the flexibility of motor learning. Much recent work has explored how the dynamics of neural populations drive movement preparation and execution^[1,2], and a natural extension of this idea is to explore how changes in neural population dynamics facilitate motor learning. Previous neurophysiological studies of motor learning, using force-field adaptation paradigms, have characterized single neuron tuning properties in PMd and M1 and discovered that many individual neurons adapt their responses to compensate for the force field^[3,4]. However, a large portion of neurons show heterogeneous responses to force field learning that are challenging to understand when we look at one neuron at a time. A different approach is to understand motor learning in a neural population dynamics framework. Yet it remains unclear how the computation for motor learning operates in the neural population. Here, we explore the changes in neural population activity that occur during curl force field adaptation as well as the spatial generalization of adapted behaviors.

We trained rhesus monkeys to adapt to a curl force field, active only during reaches to a single adaptation target in a ring of 12 targets. In addition, reaches to adjacent, non-adapted targets using an “error clamp” were interleaved with the adaptation trials when monkeys learned to compensate for the force field (Fig. 1A). Behaviorally, monkeys showed gradual adaptation to the force field as indicated by decrease in the error of hand trajectory perpendicular to the desired direction of movement (the mean deviation from a straight-line hand path, Fig. 1B). Monkeys also showed a bell-shaped spatial generalization pattern: the level of hand force difference from baseline reaches decayed as a function of target angle away from the adaptation target (Fig. 2D).

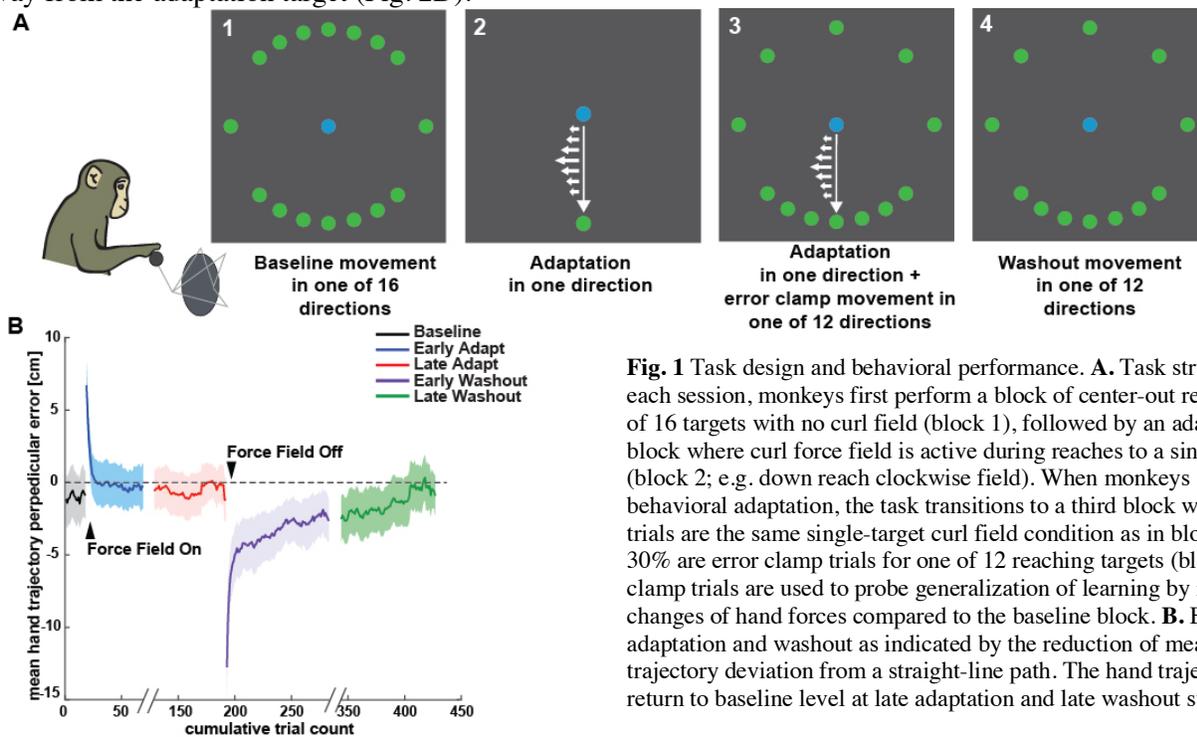


Fig. 1 Task design and behavioral performance. **A.** Task structure. In each session, monkeys first perform a block of center-out reaches to one of 16 targets with no curl field (block 1), followed by an adaptation block where curl force field is active during reaches to a single target (block 2; e.g. down reach clockwise field). When monkeys show behavioral adaptation, the task transitions to a third block where 70% trials are the same single-target curl field condition as in block 2 and 30% are error clamp trials for one of 12 reaching targets (block 3). Error clamp trials are used to probe generalization of learning by measuring changes of hand forces compared to the baseline block. **B.** Behavioral adaptation and washout as indicated by the reduction of mean hand trajectory deviation from a straight-line path. The hand trajectory errors return to baseline level at late adaptation and late washout stages.

We recorded neural activity in PMd and M1 during adaptation and found two patterns of systematic changes in population activity patterns before movement initiation and during movement execution:

Pattern 1: gradual adaptation and generalization of learning are reflected in a 2D neural subspace

First, using the targeted dimensionality reduction approach^[5], we projected preparatory neural population activity (200-300 ms before movement initiation) into a 2D subspace where we found neural states were radially organized according to reach direction. In this subspace, the neural state for the adaptation target shifted towards that of the adjacent target opposite the direction of the curl field (measured before adaptation), and the shift distance of neural states was correlated with the change of perpendicular hand force in the first 100 ms after movement initiation (Fig. 2A,B). The neural states for nearby targets showed similar shifts towards their adjacent target states; the amount shifted diminished with a similar spatial profile to the behavioral generalization (Fig. 2C-E). These results demonstrate the correlation between hand force

and neural states during curl field adaptation, as well as a neural population correlate of motor learning generalization.

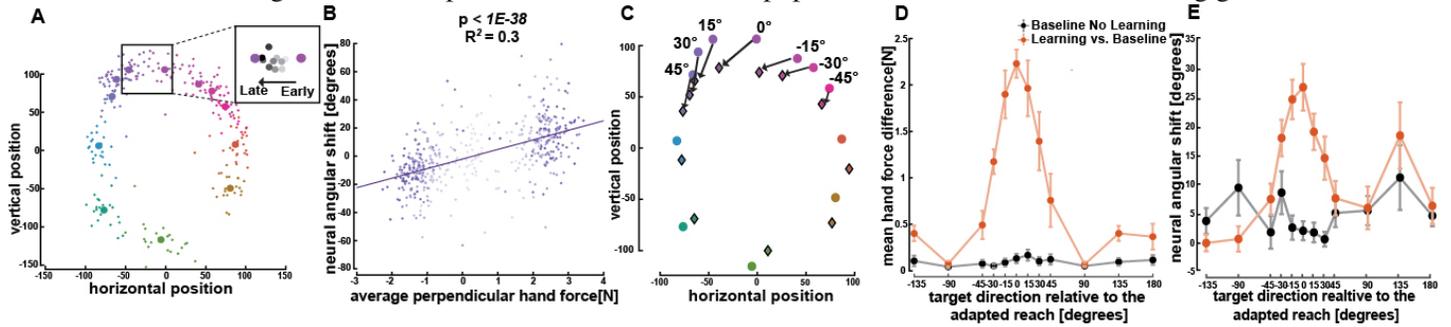


Fig.2 Shift of preparatory neural states in a 2D subspace shows gradual adaptation and generalization of learning. **A.** In this 2D subspace, neural states are radially organized as a ‘ring’ corresponding to reach directions in the baseline block. The inset shows the gradual shift of neural states (gray circles) from the baseline state of the ‘adaptation’ target (magenta circle) to that of its adjacent target (purple circle). **B.** The neural state angular shift along the ‘ring’ during adaptation to a clockwise and a counterclockwise curl force field is correlated with the gradual change of perpendicular hand force in the first 100ms after movement initiation ($p < 1E-38$, $R^2 = 0.3$). Lighter dots correspond to earlier adaptation trials and darker dots later trials. **C.** Neural states for reaches to nearby targets shift radially and opposite the direction of the curl field (here is an example of adaptation to a clockwise curl field). Circles are baseline neural states and diamonds are neural states in error clamp block. **D.** Behavioral generalization measured by changes of hand force shows bell-shaped pattern. **E.** Generalization of the neural states in the 2D subspace also shows bell-shaped pattern similar to behavioral generalization.

Pattern 2: shift of neural states in a third dimension and learning of new neural state repertoire

Second, during curl field learning, neural states for the adaptation target gradually shifted in a third dimension away from the baseline states (Fig. 3A,B). We observed a similar shift of neural states for all targets in error clamp trials (Fig. 3A). This result is intriguing because it also occurred to reaching targets far from the adaptation target for which no behavioral adaptation was observed. This suggests that the neural population generates a global change of activity correlated with the process of curl field adaptation but the change is not specific to the adapted reach.

Furthermore, the separation of neural states in the baseline and error clamp blocks in this third dimension indicates that the neural population explored a different repertoire of activity patterns after curl field learning. We found neural repertoire change, quantified by the dissimilarity between neural state clusters, for both preparatory and movement neural states: preparatory states after learning were outside the domain of the before-learning preparatory states, and movement states after learning were outside the domain of the before-learning movement states (Fig. 3C, $p < 0.0001$). These results suggest that the neural population may utilize distinct activity patterns in the context of curl force field learning in a categorically different way from the “reassociation” strategy found in a short-term brain-computer interface learning context^[6].

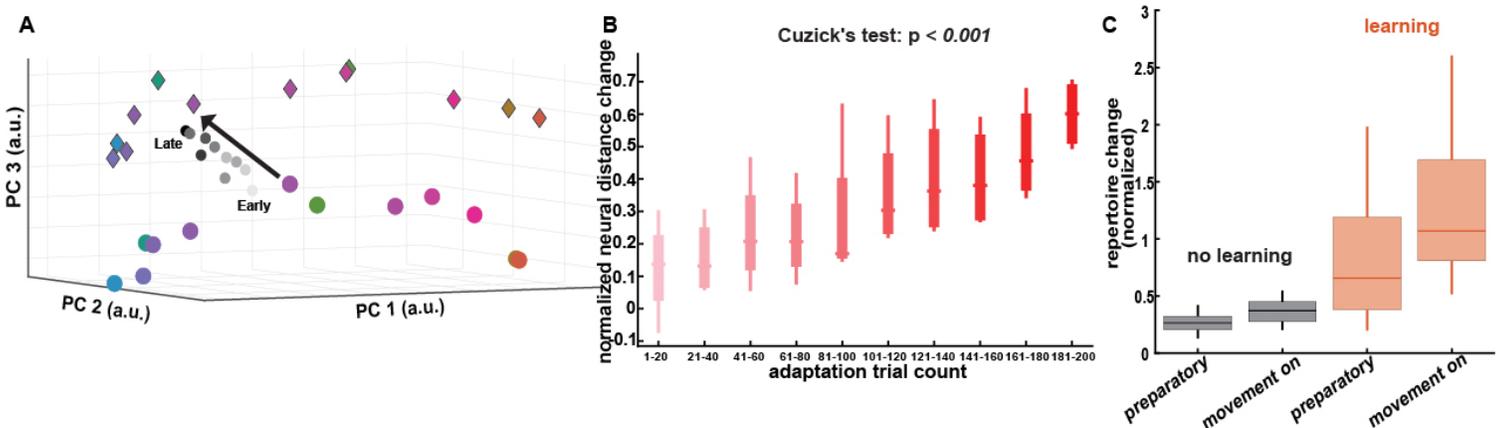


Fig. 3 A. Visualization of the gradually shifted neural states (gray circles) for the adaptation target away from the baseline states (color circles) and towards a new neural state repertoire in the error clamp trials (color diamonds). **B.** Quantification of neural state shift along the axis that best separates baseline and error clamp trial neural states ($p < 0.001$). **C.** Neural repertoire change is quantified by assessing the distances between each post-learning neural activity pattern in the error clamp block and its nearest neighbors among all of the baseline activity patterns. Values near zero indicate neural repertoire preservation and larger values indicate repertoire change. Black boxes are results from control sessions where monkeys did thousands of center-out reaches in the absence of a curl field; red boxes are results from curl force field adaptation sessions. To compute repertoire change for each control session, we used trials in which the trial IDs match the baseline block and error clamp block in a learning session.

Overall, these findings are a first step towards understanding how neural population activity change systematically to facilitate adaptation to novel arm dynamics. This in turn may further elucidate how neural circuits learn to adapt their activity patterns in response to changing task demands.