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Posterior parietal cortex plays a causal role in perceptual and categorical decisions

Yang Zhou* and David J. Freedman*

Posterior parietal cortex (PPC) activity correlates with monkeys' decisions during visual discrimination and categorization tasks. However, recent work has questioned whether decision-correlated PPC activity plays a causal role in such decisions. That study focused on PPC's contribution to motor aspects of decisions (deciding where to move), but not sensory evaluation aspects (deciding what you are looking at). We employed reversible inactivation to compare PPC's contributions to motor and sensory aspects of decisions. Inactivation affected both aspects of behavior, but preferentially impaired decisions when visual stimuli, rather than motor response targets, were in the inactivated visual field. This demonstrates a causal role for PPC in decision-making, with preferential involvement in evaluating attended task-relevant sensory stimuli compared with motor planning.

ecision-making requires evaluating taskrelevant sensory stimuli to select appropriate motor responses. The primate posterior parietal cortex (PPC) is well suited to mediate decision-making because of its anatomical position at a midpoint in the sensorycognitive-motor cortical hierarchy (1-3). Indeed, there is a correlation between PPC activity and monkeys' decisions during visual discrimination and categorization tasks (4-12). Much of this previous work has focused on the lateral intraparietal area (LIP) (13-15). Yet, PPC's role in sensory stimulus evaluation and motor planning aspects of decisions has been debated. Recent work showed that reversible inactivation of LIP does not affect motor aspects of decisions during a visual motion discrimination task (16). This leaves open the possibility that LIP is instead more engaged in processes related to evaluating sensory stimuli (e.g., stimulus feature processing, perceptual or abstract categorization, and selective attention), as opposed to selecting motor responses, during decision-making. Furthermore, neuronal recordings have demonstrated correlates of more flexible categorical or rule-based tasks in PPC (13), raising the possibility that the primate PPC may be more engaged in decisions requiring greater cognitive flexibility or abstraction than in the classic perceptual decision tasks.

We directly compared LIP's role in sensory stimulus evaluation and motor-planning functions during flexible visual perceptual and categorical decisions. We reversibly inactivated LIP in one hemisphere with intracortical injections of muscimol during several variants of motiondirection categorization (MDC) and motiondirection discrimination (MDD) tasks. Within each task, monkeys reported their decisions about the category membership (MDC task) or motion direction (MDD task) of a sample stimulus with a saccade to a target of the associated color (Fig. 1A). The mappings between motion categories or directions and target color were arbitrarily assigned at the start of training (and fixed across the study), with the two categories (MDC) or directions (MDD) assigned to red and green targets, respectively. Because the locations of the red and green targets were randomly interleaved across trials, there was a flexible mapping between motion category or direction and the saccade direction. In the MDC task, 10 motion directions were shown at three angular distances from the category boundary (Fig. 1B). In the MDD task, two directions of motion were shown, each at three levels of coherence (i.e., signal to noise). To assess LIP's contribution to stimulus evaluation and motor planning, each task was tested in blocks of trials using three spatial configurations of motion stimuli and saccade targets with respect to the location of the inactivated visual field (IVF) contralateral to muscimol injection (Fig. 1C). In the "Stimulus IN" (S_{IN}) condition, the motion stimulus was shown within the IVF, with both saccade targets outside the IVF. In the "Target IN" $(T_{\rm IN})$ condition, the motion stimulus was outside the IVF and one of the colored saccade targets was shown in the IVF. In the "Both OUT" (BOUT) condition, neither the motion stimuli nor the saccade targets were in the IVF.

We examined the impact of LIP inactivation on evaluating visual motion in the $S_{\rm IN}$ condition (Fig. 2). LIP inactivation produced a significant behavioral impairment in both the MDC and MDD tasks, shown by a decrease in overall accuracy (Fig. 2, A, E, G, and K; MDC: $P_{(\rm accuracy)} = 2.2e-08, t_{(37)} = -7.1$; MDD: $P_{(\rm accuracy)} =$ 5.8e-11, $t_{(37)} = -9.1$, inactivation versus control, unpaired *t* test) and increase in reaction time (RT) (Fig. 2, B, F, H, and L) (MDC: $P_{(RT)}$ = 0.0062, $t_{(37)} = 2.9$; MDD: $P_{(RT)} = 0.0011$, $t_{(37)} =$ 3.5, unpaired t test). In both tasks, a greater behavioral impairment was observed for one of the motion categories or directions (fig. S1; MDC: P = 6.8e-04, $t_{(16)} = 4.2$; MDD: P = 0.0048, $t_{(16)} = 3.3$, paired t test). Psychometric curve fitting showed a significant change in bias and an increase in psychophysical threshold during both tasks (Fig. 2, M to P, and fig. S2; MDC: $R^{2}_{\text{(inactivation)}} = 0.90 \pm 0.034, R^{2}_{\text{(control)}} = 0.94 \pm$ 0.044, $P_{\text{(bias)}} = 2.7\text{e-}04$, $t_{(37)} = 4.0$, $P_{\text{(threshold)}} =$ 1.9e-08, $t_{(37)} = 7.1$; MDD: $R^2_{(\text{inactivation})} = 0.91 \pm$ 0.069, $R^2_{\text{(control)}} = 0.98 \pm 0.025$, $P_{\text{(bias)}} = 9.5\text{e-}4$, $t_{(37)} = 3.6, P_{(\text{threshold})} = 1.2e-7, t_{(37)} = 6.5, \text{ un-}$ paired t test). Behavioral impairments in the $S_{\rm IN}$ condition of both tasks were significantly greater than those in the B_{OUT} condition (Fig. 2, E, F, K, and L; MDC: $P_{(\text{accuracy})} = 7.5e-06, t_{(16)} =$ $-6.5, P_{(\text{RT})} = 0.0011, t_{(16)} = 4.0; \text{ MDD: } P_{(\text{accuracy})} =$ 1.1e-09, $t_{(16)} = -12.6$, $P_{(RT)} = 1.9e-04$, $t_{(16)} = 4.8$, S_{IN} versus B_{OUT} , paired t test), in which we did not observe a global impact on accuracy (Fig. 2, C, E, I, and K; MDC: $P_{(\text{accuracy})} = 0.17, t_{(37)} = -1.4;$ MDD: $P_{(\text{accuracy})} = 0.12, t_{(37)} = -1.6$, inactivation versus control, unpaired t test) or RT (Fig. 2, D, F, J, and L; MDC: $P_{(\text{RT})} = 0.60, t_{(37)} = 0.53;$ MDD: $P_{(RT)} = 0.71$, $t_{(37)} = 0.37$, unpaired t test).

LIP's role in motor aspects of decisions was assessed in the $T_{\rm IN}$ condition (Fig. 3), which is the spatial configuration nearly always tested in past studies of LIP with the MDD task (7, 8, 12, 14, 15, 17) [but see (18)]. Although the motion stimulus was outside the IVF, note that the $T_{\rm IN}$ condition did require evaluating the color of the in-IVF saccade target. After LIP inactivation, the monkeys' saccadic choices were significantly biased away from the IVF in both tasks (Fig. 3, A, C, G, and I; MDC: P = 1.3e-07, $t_{(16)}$ =8.9, MDD: P = 3.0e-04, $t_{(16)}$ = -5.4, paired t test), and a greater RT increase was observed on trials in which the saccade was directed toward versus away from the IVF (Fig. 3, B, D, H, and J; MDC: P = 7.0e-06, $t_{(16)} = -6.5$, MDD: $P = 6.0e-05, t_{(16)} = 4.6$, paired t test). Although LIP inactivation produced an ipsilateral saccade bias, there was no significant difference in mean accuracy between inactivation and control sessions for either task (Fig. 3, A, E, G, and K; MDC: $P = 0.13, t_{(37)} = -1.5;$ MDD: $P = 0.56, t_{(37)} = -0.59,$ unpaired t test), and accuracy on both tasks was less influenced by inactivation in $T_{\rm IN}$ than by that in S_{IN} (Fig. 3, E and K; MDC: P = 1.6e-08, $t_{(16)} = -10.4$; MDD: P =1.2e-06, $t_{(16)} = -7.5$, paired t test). The magnitudes of RT effects between $T_{\rm IN}$ and $S_{\rm IN}$ were statistically indistinguishable (Fig. 3, F and L; MDC: P = 0.40, $t_{(16)} = 0.86$; MDD: P = 0.093, $t_{(16)} = 1.8$, paired t test). Psychometric curve fitting showed a significant bias in saccades away from the IVF in both tasks, but no increase in $T_{\rm IN}$ threshold in either task (Fig. 3, M to P, and fig. S3; MDC: $R^2_{(\text{inactivation})} =$ $0.92 \pm 0.070, R^2_{(\text{control})} = 0.94 \pm 0.047, P_{(\text{bias})} =$ 4.0e-07, $t_{(37)} = 6.1$, $P_{(\text{threshold})} = 0.15$, $t_{(37)} = 1.5$; MDD: $R^{2}_{(\text{inactivation})} = 0.98 \pm 0.010, R^{2}_{(\text{control})} =$ $0.98 \pm 0.010, P_{\text{(bias)}} = 0.0013, t_{(37)} = 3.5, P_{\text{(threshold)}} =$ 0.33, $t_{(37)} = 0.99$, unpaired t test). These effects

Department of Neurobiology, The University of Chicago, Chicago, IL 60637, USA. *Corresponding author. Email: yangz1@uchicago.edu (Y.Z.);

^{*}Corresponding author. Email: yangzi@uchicago.edu (Y.Z.) dfreedman@uchicago.edu (D.J.F.)

were consistent across monkeys (figs. S4 and S5).

We examined how distinct components of the decision process were affected by inactivation. We fitted our results with fixed-boundary drift diffusion models, which captured monkeys' decision behavior across different task conditions in both the MDD and MDC tasks, including both accuracy and the RT distributions (figs. S6 and S7). This revealed that LIP inactivation substantially slowed the evidence accumulation process (drift rate) only in $S_{\rm IN}$, while appreciably changing the saccade choice bias (starting point of the diffusion process) and decision boundary only in $T_{\rm IN}$ across monkeys and tasks (tables S1 to S4). Inactivation also did not produce substantial impairments of gaze position, microsaccades, or peak saccade velocity (figs. S8 to S10).

We hypothesized that the inactivation-related behavioral deficits in the $S_{\rm IN}$ condition of the MDD task were due to disrupting neuronal activity related to evaluating stimulus motion within the IVF. Thus, we recorded from 194 LIP neurons (monkey M: n = 78; monkey B: n =116) during the $S_{\rm IN}$ condition, targeting the same cortical locations within the same hemispheres as in the inactivation experiments. More than half of LIP neurons (monkey M: 50/78, monkey B: 54/116) showed significant motion direction selectivity (DS) in the MDD task (one-way ANOVA, P < 0.01). DS emerged before the monkeys' mean RTs (fig. S11A), and the magnitude of DS was positively correlated with motion coherence at the single-neuron and population levels, but did not converge to a fixed threshold near the decision time (Fig. 4, A to D, and fig. S11B). Neuronal activity on zero-coherence motion trials (in which monkeys could only guess about motion direction) reflected the monkeys' trial-by-trial decisions, consistent with a role in the decision process. Decision-correlated activity across all motion-coherence levels was evident in single-neuron activity (Fig. 4, A and B, and fig. S12) and in the LIP population (Fig. 4C; see fig. S13 for results reported separately for each monkey) and was confirmed using a receiver operating characteristic (ROC) analysis (Fig. 4D).

To further test whether DS in LIP was decision related, we compared activity on correct versus error low-coherence trials (see materials and methods). LIP population activity was more similar in trials in which monkeys decided that different motion directions were the same versus trials in which the same motion directions were treated as different (Fig. 4E; P = 1.9e-04, $t_{(100)}$ = 3.9, paired t test). Accordingly, LIP activity covaried more closely with the monkeys' trial-by-trial decisions about motion direction than it did with the physical motion direction (Fig. 4F; P = 6.8e-04, $t_{(100)} = -3.4$, paired t test, comparing ROC values on chosen versus physical direction of motion). Furthermore, LIP activity covaried with the monkeys' RTs, with most neurons showing a greater response to their preferred motion direction on shorter versus longer RT trials for all motion-coherence levels (and a weaker response to their nonpreferred direction; figs. S14 and S15). Even in low-coherence (Fig. 4G) and zero-coherence (Fig. 4H) trials, DS evolved more rapidly on shorter versus longer RT trials (comparing slope: $P_{(low)} < 0.01$, $P_{(zero)} <$ 0.01, bootstrap). At the population level, the slope of DS negatively correlated with monkeys' RT (fig. S15; r = -0.9455, P = 0.0044). Elevated DS was even observed before stimulus onset on lowcoherence trials (Fig. 4H), suggesting that the state of LIP activity before stimulus onset was predictive of the monkeys' upcoming decision in that trial. Furthermore, a partial correlation analysis examined choice- and stimulus-related components of DS (i.e., $r_{(choice)}$ and $r_{(stimulus)}$; Fig. 4I and fig. S16) (19). This revealed that the choice and stimulus components of LIP DS were positively correlated (Fig. 4J, r = 0.6276, P < 0.0001).

Taken together, our results suggest that LIP plays an important role in visually based perceptual and categorical decisions, with preferential involvement in stimulus evaluation compared with motor-planning aspects of such decisions. This idea is supported by behavioral impairments on discrimination and categorization tasks caused by reversibly inactivating LIP, neurophysiological recordings revealing decision correlated LIP activity during the MDD task, as well as work from multiple groups showing sensory-decision-related LIP activity in several tasks (11, 13, 20), including categorization (6, 9). Both tasks tested in this study had a flexible mapping between the decisions about motion stimuli and the direction of the saccade used to report those decisions. Thus, it will be interesting to determine whether LIP plays a similar role during tasks with fixed sensorymotor mappings.

It is well established that LIP helps to mediate covert spatial attention (21-23) and saccades (1, 24, 25). However, the current study highlights LIP's role in evaluating the abstract behavioral significance of visual stimuli during decision-making. Although attention contributes toward the selection and representation of taskrelevant stimuli, and disruption of attention by LIP inactivation may contribute to the current results, our inactivation results in the S_{IN} condition are unlikely to arise primarily from disrupting attention- or saccade-related functions for several reasons. First, the LIP neurons targeted for inactivation showed activity that correlated with MDD task decisions, indicating that LIP's role extends beyond the comparatively fixed representation of motion direction in the middle temporal (MT) area (4, 6, 11, 14, 16). The







Fig. 2. Causal evidence for decision-related sensory evaluation in LIP. (**A**) Psychometric curves for the S_{IN} condition of the MDC task. Task accuracy pooled across both monkeys is plotted as the proportion of choosing the primary category, defined as the category for which each monkey showed a greater decrease in accuracy (on average across all sessions) after LIP inactivation (figs. S4 and S5 show data for each monkey separately). (**B**) Chronometric curves are shown for the S_{IN} condition of the MDC task. (**C** and **D**) The psychometric and chronometric curves in the B_{OUT} condition of the MDC task [same format as (A) and (B)]. (**E** and **F**) Comparisons of the averaged behavioral deficits after LIP inactivation in the S_{IN} and B_{OUT} conditions of the MDC task. (**G** to **L**) Monkeys' behavioral performance in the MDD task is plotted for inactivation and control sessions. Psychometric and chronometric curves for the S_{IN}

[(G) and (H)] and B_{OUT} [(I) and (J)] conditions are shown in the same format as for the MDC task [(A) to (D)]. Monkeys showed a significantly greater deficit in the S_{IN} than in the B_{OUT} condition in the MDD task [(K) and (L)]. (**M** to **P**) Paired comparisons between inactivation and control sessions for choice bias and threshold in the S_{IN} conditions of the MDC task (M) and (N)] and the MDD task [(O) and (P)]. The open and filled symbols denote the inactivation sessions in which the majority of the recorded neurons at the targeted cortical locations preferred the primary (open) and nonprimary (filled) category or direction, respectively (see the supplementary materials). Asterisks indicate statistical significance: *P < 0.05, **P < 0.01, ***P < 0.001, unpaired *t* test, multiple tests in [(A) to (D)] and [(G) to (J)] are Bonferroni corrected. The error bars denote ± SEM. P, primary; NP, nonprimary; cat, category; dir, direction; H, high; M, middle; L, low.

partial correlation analysis suggests that LIP DS may be more closely choice correlated compared with other parietal areas (19, 26), although a direct comparison across multiple areas during the same tasks will be needed. Second, inactivation produced greater impairments for specific directions and categories, rather than uniformly affecting performance, and we found similar results when we analyzed inactivation behavioral data with respect to neurons' stimulus preferences at the targeted LIP sites (figs. S17 and S18). This may relate to biased representations of categories and directions observed in LIP during the MDD and MDC tasks (27), or it could reflect anatomical clustering of such representations in LIP. Third, LIP inactivation did not produce an obvious impairment of eve movements or profound spatial neglect, although we did observe a mild ipsilateral bias during the free choice saccade task (fig. S19), consistent with previous studies (16, 23, 28). Nevertheless, future work using more precise causal approaches such as stimulating or silencing pools of neurons with specific direction or category preferences can more precisely dissect LIP's contributions toward decision-making tasks.

A recent study came to a different conclusion regarding LIP's role in perceptual decisions, finding no apparent impact of inactivation on MDD task performance (*16*). However, that

Fig. 3. Causal evidence for decisionrelated saccade planning in LIP. (A) Psychometric curves for T_{IN} condition of MDC task. The choice accuracy is plotted as the proportion of contralateral saccades relative to the inactivated hemisphere. Data from both monkeys were pooled based on target location. (B) Chronometric curves for the $T_{\rm IN}$ condition of the MDC task. (C and D) Comparisons of behavioral impairments after LIP inactivation between ipsilateral and contralateral target trials in the T_{IN} condition. Monkeys' saccade choices were biased toward the ipsilateral target after LIP inactivation, as shown by both accuracy (C) and RT (D). (E and F) Comparisons of overall behavior deficits after LIP inactivation between the S_{IN} and T_{IN} conditions of the MDC task. Monkeys showed significantly greater behavioral impairment in the S_{IN} condition than in the T_{IN} condition in accuracy (E) but not RT (F). (G to L) Monkeys' behavioral performance in the \mathcal{T}_{IN} condition of the MDD task. Psychometric and chronometric curves [(G) and (H)] are in the same format as those in the MDC task [(A) and (B)] Monkeys showed consistent saccadic choice biases after LIP inactivation in both the MDD and MDC tasks [(I) and (J)]. In the MDD task, a greater deficit was observed after LIP inactivation in the SIN than in the T_{IN} condition in accuracy (K)

study only considered LIP's contributions to motor-planning $(T_{\rm IN})$ aspects of the MDD task, not sensory stimulus evaluation (S_{IN}) . Another study found that LIP activity was decision correlated in both S_{IN} and T_{IN} conditions of an MDD task but concluded that LIP activity correlated more closely with motor aspects (however, that study did not directly test LIP's causal contributions) (18). Consistent with the earlier inactivation study, we found that LIP inactivation did not impair average MDD-task accuracy in the $T_{\rm IN}$ condition. However, we did observe a saccade bias away from the IVF in the $T_{\rm IN}$ condition, suggesting a deficit in mapping decisions to actions. Several factors may account for this discrepancy. First, we used an RT rather than a fixed-interval version of the MDD task, perhaps prompting different strategies or speed-accuracy tradeoffs. Second, our tasks employed a flexible mapping (based on saccade target color) between motion stimuli and saccades. Thus, LIP may have been more engaged by decisions requiring greater cognitive flexibility or abstraction. Furthermore, the $T_{\rm IN}$ condition in our tasks required discriminating the color of the in-IVF saccade target to plan the correct saccade, so that condition had greater sensory evaluation demands than the traditional MDD task (13). Compared with the previous study, our animals learned both the MDD and MDC tasks, and the strategy used to solve the MDD task could have been affected by MDC training. The greater behavioral deficit observed in the MDD task (which employed low-coherence motion stimuli) compared with the MDC task (which used only 100% coherent motion) is consistent with LIP integrating noisy sensory evidence (12, 14, 17), and the saccadic choice bias in the $T_{\rm IN}$ condition supports LIP's involvement in mediating the saccades used for reporting decisions (14, 29). Thus, decision-related motion encoding might be transformed into saccadic signals via coordination between sensory and motor pools of LIP neurons, in contrast to LIP reading out sensory inputs exclusively from upstream visual areas such as MT (30).

Perceptual and categorical decisions rely on contributions from and coordination among a network of cortical and subcortical areas spanning the sensory, cognitive, and motor hierarchy (13–15, 31, 32). Although the current study establishes primate PPC as an important node in that network, along with recent work in rodents (33–35), a more complete understanding necessitates the characterization of local and longrange circuits—within different animal models and humans—that flexibly transform sensory encoding into decisions and actions and the process by which task-related neuronal encoding emerges during learning.



but not RT (L). (**M** to **P**) Paired comparisons between inactivation and control sessions for choice bias and threshold in the T_{IN} condition of the MDC task [(M) and (N)] and the MDD task [(O) and (P)]. Asterisks indicate statistical significance in the same way as in Fig. 2.



Fig. 4. LIP activity reflects decision-related sensory evaluation.

(A and B) Activity is shown for each motion-coherence level for two example direction-selective LIP neurons in the MDD task. The motion stimulus but not the targets appeared in neurons' RF. The zero-coherence trials were grouped based on the monkeys' choices. The two vertical dashed lines mark the time of target and motion stimulus onset, respectively. (C) Average normalized population activity across all direction-selective neurons is shown for each motion-coherence level, aligned to stimulus onset (left panel) or saccade onset (right panel). Activity shown in the left panel is truncated at the monkeys' mean RT for each coherence level.
(D) The DS (determined by ROC) for the different coherence levels is shown as in (C). (E) Average activity on low-coherence trials is shown for neurons' preferred and nonpreferred directions, separately for correct and error trials. (F) Neuronal selectivity on low-coherence

trials is compared for the monkeys' decisions about motion direction compared with the physical direction of stimulus motion. Asterisks indicate time periods in which there was a significant difference (P < 0.01, paired t test). (**G** and **H**) DS on low-coherence trials (G) and choice selectivity (CS) on zero-coherence trials (H) is compared between shorter RT and longer RT trials. Shaded areas denote \pm SEM. (**I** and **J**) Partial correlation analysis. (I) The value of $r_{(stimulus)}$ (the partial correlation between neuronal activity and stimulus direction, given the monkeys' choices) and $r_{(choice)}$ (the partial correlation between neuronal activity and monkeys' choice, given the stimulus direction) are plotted across time. (J) Correlation between $r_{(stimulus)}$ and $r_{(choice)}$. Note that most LIP neurons showed a congruent sign between $r_{(stimulus)}$ and $r_{(choice)}$ values. P, preferred; NP, nonpreferred; H, high; M, middle; L, low; Z, zero; C, correct; E, error.

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ACKNOWLEDGMENTS

We thank J. Assad, N. Masse, K. Latimer, K. Mohan, and W. Johnston for their comments on an earlier version of this manuscript. We also thank the veterinary staff at The University of Chicago Animal Resources Center for expert assistance. **Funding:** This study was supported by National Institutes of Health grant no. NIH R01EY019041. **Author contributions:** Y.Z. and D.J.F. designed the experiments and wrote the manuscript. Y.Z. trained monkeys, collected the behavioral and neuronal data, analyzed the data, and made the figures. D.J.F. supervised the project. **Competing interests:** The authors declare no competing financial interests. **Data and materials availability:** All data and analyses necessary to understand and assess the conclusions of the manuscript are presented in the main text and in the supplementary materials. Data and analysis code from this study are available at Figshare (36).

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/365/6449/180/suppl/DC1 Materials and Methods Figs. S1 to S19 Tables S1 to S4 References (37–46)

29 January 2019; accepted 18 June 2019 10.1126/science.aaw8347



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Science **365** (6449), 180-185. DOI: 10.1126/science.aaw8347

Perceptual decision-making in primates

Past investigations of the posterior parietal cortex (PPC) in perceptual decisions tested only its contribution to motor aspects of decisions. However, Zhou and Freedman tested the primate PPC's role in both sensory and motor aspects of decisions. Inactivation of the lateral intraparietal area strongly impaired sensory processing aspects of decision-making, more so than motor aspects. Lateral intraparietal area neurons targeted for inactivation were highly correlated with the monkeys' trial-by-trial decisions about stimuli in the neurons' receptive fields. Thus, the posterior parietal cortex is indeed involved in decision-making but plays a more sensory role than predicted. *Science*, this issue p. 180

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