# Dorsal pulvinar inactivation leads to spatial selection bias without perceptual deficit

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Running Head: Pulvinar inactivation during perceptual decision

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# Abstract

Dorsal pulvinar has been implicated in visuospatial attentional and perceptual confidence processing. Perturbations of the dorsal pulvinar also induce an overt spatial saccade bias during free choices. But it remains unclear whether the dorsal pulvinar inactivation during an oculomotor target selection based on a perceptual decision will lead to perceptual impairment or a more general orienting deficit. To address this question, we reversibly inactivated unilateral dorsal pulvinar by injecting GABA-A agonist THIP while two macaque monkeys performed a color discrimination saccade response task with varying perceptual difficulty. We used Signal Detection Theory to dissociate perceptual discrimination (dprime) and spatial selection bias (response criterion) effects. We expected a decrease in dprime if dorsal pulvinar affects perceptual discrimination and a shift in response criterion if dorsal pulvinar is mainly involved in spatial orienting. After inactivation, we observed response criterion shifts away from contralesional stimuli, especially when two competing peripheral stimuli in opposite hemifields were present, for both difficulty levels. The saccade latency for the contralesional selection increased under all conditions. Notably, the dprime and overall accuracy remained largely unaffected. Our results underline the critical contribution of the dorsal pulvinar to spatial orienting while being less important for perceptual discrimination.

# Introduction

Visual scenes contain multiple spatial locations, serving as potential saccades targets. Selecting a target in complex scenes requires efficiently perceiving and evaluating behaviorally relevant information at different spatial locations. Many studies investigating the neural processes of visuospatial target selection emphasize interactions in frontoparietal cortical networks (Corbetta and Shulman, 2011; Fiebelkorn et al., 2018; Adam et al., 2020). These direct cortical connections are paralleled by indirect routes through the higher-order thalamic nuclei such as the pulvinar, raising the question of how the pulvinar contributes to the selection of behaviorally relevant stimuli in space to guide visuospatial decision-making.

The primate pulvinar consists of several nuclei with distinct functional properties and connectivity profiles. The dorsal part of the pulvinar (dPul) encompasses the medial pulvinar and the dorsal part of the lateral pulvinar (Gutierrez et al., 2000; Stepniewska, 2003; Arcaro et al., 2015; Baldwin and Bourne, 2017). These nuclei developed together with the association cortices in the course of primate evolution and are reciprocally connected to the parietal and prefrontal cortex, orbitofrontal cortex, insula, cingulate, superior and inferior temporal cortex (Kaas and Lyon, 2007; Preuss, 2007; Kaas and Baldwin, 2020). This extensive connectivity profile identifies the dorsal pulvinar as a unique brain hub well situated to interact with and modulate the circuitry involved in spatial attentional orienting and target selection (Grieve et al., 2000; Sherman and Guillery, 2002; Shipp, 2003; Saalmann and Kastner, 2015; Bourgeois et al., 2020; Kagan et al., 2021). Studies in human patients with unilateral thalamic lesions encompassing the pulvinar demonstrated deficits related to orienting or responding to perceptually or behaviorally salient stimuli in the contralesional hemifield (Danziger et al., 2001; Karnath et al., 2002; Arend et al., 2008b, 2008a; Lucas et al., 2019). Similar to neglect/extinction in patients, monkey studies using targeted reversible unilateral pharmacological inactivation and electrical microstimulation of the dorsal pulvinar induced contralesional visuospatial deficits (Petersen et al., 1987; Desimone et al., 1990; Wilke et al., 2010, 2013; Komura et al., 2013; Dominguez-Vargas et al., 2017). Such deficits manifest behaviorally in several ways. First, the inactivation causes impairment of spatial attentional orienting to cued targets in contralesional hemifield, decreasing performance in detection or color-contingent manual response tasks (Petersen et al., 1987; Desimone et al., 1990). Second, the confidence about contralesional perceptual categorization but not the coategorization itself has been reported to decrease after the inactivation, in the absence of competing distractors in the opposite hemifield (Komura et al., 2013). Third, a target selection bias away from contralesional hemifield was observed in the free-choice saccade task (Wilke et al., 2010, 2013). Such inactivation-induced bias could be alleviated by presenting only a

single target or increasing the reward for contralesional targets but less so by perceptual saliency manipulations (Wilke et al., 2013).

The above causal perturbation findings, and the results of electrophysiological recordings (Robinson and Petersen, 1992; Benevento and Port, 1995; Bender and Youakim, 2001; Dominguez-Vargas et al., 2017; Fiebelkorn et al., 2019; Schneider et al., 2019, 2021), on the one hand, implicate dPul in attentional allocation and perceptual processing, but on the other, are also compatible with a role in more general spatial orienting bias. Different task demands might be one reason for such interpretational ambiguity. In particular, studies that used attentional cueing and perceptual discrimination employed spatially-dissociated from visual stimuli manual responses (e.g. button presses). At the same time, our previous choice tasks always required a saccade towards a peripheral target and did not involve difficult perceptual discrimination (Wilke et al., 2010, 2013; Dominguez-Vargas et al., 2017). Therefore, it remains unclear if perceptual factors contribute to contralesional visuospatial deficits in conditions of spatial competition and target-congruent saccade actions.

We used a color discrimination saccade selection task to address this question with two essential new features. Firstly, we included easy and difficult (i.e. perceptually similar to a target) distractors that should not be selected with a saccade. Secondly, we introduced an option to maintain central fixation as a correct response when only distractor(s) were presented. The task involved three different stimulus types – single stimuli, double “same” stimuli (target-target or distractor-distractor) and double different stimuli. Single stimuli included a peripheral target or a distractor and a central fixation option, resulting in low spatial competition. The double stimuli included left and right peripheral stimuli and a fixation option, adding competition between hemifields. Using the Signal Detection Theory, we investigated whether unilateral dPul inactivation leads to a perceptual deficit or a spatial selection bias. Suppose the dorsal pulvinar is mainly involved in spatial orienting. In that case, we expected a shift in the criterion manifesting as the selection bias away from the contralesional hemifield, regardless of whether a target or a distractor is presented. But if the dorsal pulvinar is involved in discriminating targets from distractors, we expected a contralesional perceptual sensitivity deficit, manifesting as a decrease in dprime. Furthermore, if dPul is mainly relevant for regulating the competition between hemifields, we expected a more substantial effect of inactivation in double stimuli conditions.

# Methods

## Experimental procedures

All experimental procedures complied with the ARRIVE guidelines (https://arriveguidelines.org) and were conducted in accordance with the European Directive 2010/63/EU, the corresponding German law governing animal welfare, and German Primate Center institutional guidelines. The procedures were approved by the responsible government agency (Niedersaechsisches Landesamt fuer Verbraucherschutz und Lebensmittelsicherheit (LAVES), Oldenburg, Germany).

Two adult male rhesus monkeys (*Macaca mulatta*), weighing 9 kg and 10.5 kg, served as subjects (monkey 1, Cornelius, M1; monkey 2, Curius, M2). For both monkeys, the surgical procedures for implanting an MRI-compatible headpost and chambers, and small within-chamber craniotomies, were the same as described in Dominguez-Vargas et al. (2017). The inactivation locations in the dorsal pulvinar were estimated based on anatomical MRI as described in more detail in the previous work (Dominguez-Vargas et al., 2017; Kagan et al., 2021). Based on the MRI images, we planned where to target the dorsal pulvinar (the grid hole and depth) based on the anatomical MR image using the Planner (Ohayon and Tsao, 2012) and BrainVoyager (Version 2.4.2, 64-bit; Brain Innovation). To confirm the inactivation locations, we performed MRI contrast agent gadolinium injections (**Figure 1A**).

The neural activity in the dorsal pulvinar was reversibly suppressed using the GABA-A agonist 4,5,6,7-tetrahydro isoxazole [5,4-c]-pyridine-3-ol (THIP hydrochloride; Tocris). The THIP was dissolved in phosphate-buffered saline (PBS). The solution (pH 7.0-7.5) was sterile filtered with a hydrophobic PTFE membrane filter (pore size: 0.2 µm, Sartorius) before injection via a sterile 31 gauge sharp-tip steel cannula (Plastics One). The solution was delivered at a rate of 0.25 µl/min using a 0.1 ml glass-tight Hamilton syringe driven by a digital infusion pump (Harvard Apparatus). The injection volume per session was 4.5-5 µl of 10 mg/ml of THIP for monkey 1 (dPul in the left hemisphere) and 1.5 µl for monkey 2 (dPul in the right hemisphere). The injected volume was determined for each monkey separately in pilot sessions in which the monkey could perform the task without nystagmus and showed an ipsilesional spatial bias for target-target (free choice) stimuli as in prior reports (Wilke et al., 2010, 2013). The selection bias during target-target trials demonstrated a successful inactivation procedure.

Every experimental session started with a pre-injection testing period, followed by the injection, a 30-40 min waiting period, and the post-injection testing period. We conducted 7 inactivation sessions interleaved with 7 control (no actual injection) sessions for each monkey. In total, M1

perfomed 15222 trials and M2 performed 10945 trials. The control sessions were performed with the same timing of events.

## Behavioral paradigm

The monkeys were sitting in a dark room in a custom-made primate chair with the head restrained 30 cm away from a 27" LED display (60 Hz refresh rate, model HN274H, Acer Inc. USA). The gaze position of the right eye was monitored at 220 Hz using an MCU02 ViewPoint infrared eye tracker (Arrington Research Inc. USA). A MATLAB-based task controller (https://github.com/dagdpz/monkeypsych, MATLAB version R2012b, The MathWorks, Inc., USA) and the Psychophysics Toolbox (Brainard, 1997) were used to control stimulus presentation.

**Color discrimination task.** Two monkeys performed a color discrimination task (**Figure 1B**) where the perceptual difficulty was determined by the color similarity of the target (T, red) vs. distractor (D, easy – yellow, difficult – orange). Target or distractor was either presented alone or with a second stimulus (distractor or target) in the opposite hemifield, determining the level of spatial competition. Monkeys had to saccade to the target or continue fixating when only distractor (s) were presented. Each trial started with the presentation of a red fixation spot. The monkey initiated each trial by acquiring eye fixation by entering the 5° radial window around the fixation spot within 500 ms after the onset of the fixation spot. After maintaining fixation for 500-900 ms, the fixation spot turned gray, and one or two peripheral dots simultaneously appeared (go-signal). Red dots represented targets, whereas yellow and orange dots represented distractors. In conditions with a single peripheral stimulus, either one target or one distractor was presented in the left or the right hemifield. In conditions with two peripheral stimuli, the monkey was shown two dots in opposite hemifields. In double-target trials, two equally-rewarded targets were presented, and the monkey could choose either as a saccade target. In double-distractor trials, two distractors were shown, which had to be ignored by maintaining central fixation. In target-distractor trials, a target was presented with a distractor in the opposite hemifield. The monkey was required to make a saccade towards the target while ignoring the distractor. The monkey had to choose within 500 ms (target acquisition epoch). As soon as the eye position entered the 5° radial window around one of the stimuli, the stimulus was selected, and the monkey was not allowed to reverse his decision. The chosen stimulus, either the selected peripheral dot for saccade responses or the fixation spot for maintaining eye fixation, turned bright to confirm the monkey's selection. After fixating the selected stimulus for another 500 ms (target hold epoch), correct responses were followed by the reward tone, a fluid reward, and an intertrial interval (ITI) of 2000ms. Incorrect answers were followed by the error tone, no liquid reward, and an ITI of 2000ms.

All stimuli were matched in luminance (dim stimuli: 11 cd/m$^2$, bright stimuli: 35 cd/m$^2$) and size (1° diameter). Targets and distractors were displayed at one of three locations per hemifield (six locations in total) with an eccentricity of 20° of visual angle. Stimulus locations were arranged concentrically around the fixation spot at 0° (mid-left), 20° (up left), 160° (upright), 180° (mid-right), 200° (down right), and 340° (down left). They were presented on a horizontal or a diagonal axis in conditions with two peripheral stimuli. All experimental conditions (stimulus type, difficulty level, spatial location) were pseudorandomized. Trials aborted before the monkey selected a stimulus returned to the pool of trials from which the next trial was chosen randomly. Distractor colors were determined in the initial sessions of psychophysical assessment.

**Distractor color determination.** After initial training of the task with a yellow distractor, we determined the two distractor colors (yellow and orange) for the experiment based on the results of a psychophysical assessment (Monkey 1, M1: six sessions, Monkey 2, M2: six sessions). The goal of the assessment was to determine a distractor color that could be correctly discriminated from the target with 70 - 80% accuracy. Thus the monkeys performed a color discrimination paradigm with five distractor colors of different perceptual difficulty ranging from yellow (very easy, RGB [60 60 0]) to red-orange (difficult, M1: [128 11 0]; M2: [128 23 0]). All trial conditions were presented in a pseudorandomized order. The perceptual difficulty was defined as the RGB color-coded ratio between green (G) and red (R). A stimulus with a G/R ratio of 1 is a yellow distractor (60 60 0) which is perceptually very different from the target color ([128 0 0]) with a G/R ratio of 0. Given the accuracy per distractor G/R ratio, we chose an orange color as difficult distractor color (M1: G/R ratio = 0.09, M2: G/R ratio = 0.18, see Supplementary Information, **Suppl. Figure S1**). The corresponding accuracy values were fitted by the cumulative normal function using Palamedes toolbox (Prins and Kingdom, 2009) in MATLAB R 2019b (The MathWorks, Inc. USA).

**Equalizing spatial choice behavior.** Before the data collection during training sessions, the left-right choice behavior was approximately equalized by shifting the entire stimulus array (both central and peripheral stimuli) with respect to the body midline (Dominguez-Vargas et al., 2017). In each experimental session, the stimulus array was adjusted for all sessions by 0° from the mid-line for M1 and by 5° for M2.

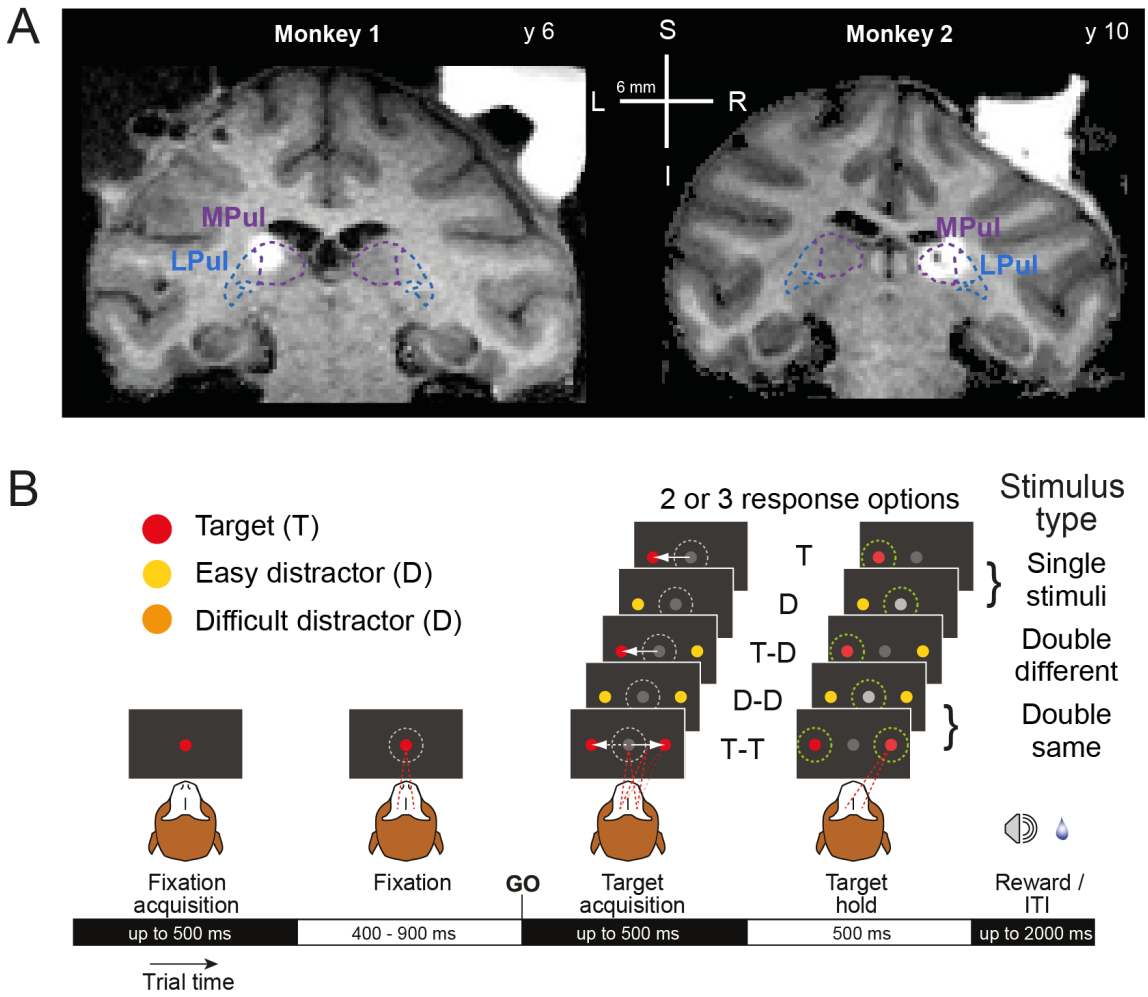


**Figure 1. Inactivation sites and task design.** (A) MR images show the inactivation sites visualized with co-injection of gadolinium MR contrast agent (ratio: 1:200 saline) ~20 min following the injection (for M1: 2 µl and M2: 3 µl, respectively) and the overlayed borders of medial pulvinar (MPul) and lateral pulvinar (LPul). (B) Two monkeys performed a color discrimination task where the perceptual difficulty was determined by the color similarity of the target (T, red) vs. distractor (D, easy - yellow, difficult - orange). Target or distractor was presented alone or with a second stimulus (distractor or target) in the opposite hemifield. Monkeys had to saccade to the target and continue fixating when only distractor(s) were presented.

# Data analysis

We analyzed the behavioral data for the “post-injection” testing period from two monkeys, with seven injections and seven control sessions for each monkey. Data analysis and statistical tests were performed using MATLAB R2015a and R. The analysis focuses on the saccade latencies, accuracy, and the Signal Detection Theory variables to evaluate if there is a significant statistical difference between control and inactivation sessions. Accuracy was defined as the proportion of correct and rewarded trials among all trials in a specific condition

(e.g. correct hits and rejections for all single stimuli trials, regardless of the hemifield). For calculating the saccade latencies, we used all completed saccades, i.e., both correct target selection and erroneous distractor selection.

## Saccade definition

All eye movements with a minimum velocity of 200 °/s and a minimum duration of 30 ms were considered saccades. To detect a saccade, the instantaneous saccade velocity was calculated sample by sample as the square root of the sum of squared interpolated (220 Hz to 1 kHz) and smoothed (12 ms moving average rectangular window) horizontal and vertical eye position traces. These data were smoothed again (12 ms moving average rectangular window). Saccade onset was defined as the first eye position change after the go-cue that exceeded a velocity threshold of 200°/s. Saccade offset was defined as the first point in time when eye velocity dropped below 50°/s after saccade onset.

## Signal detection theory

To address our two alternative hypotheses, whether the contralesional visuospatial deficit is a consequence of a contralesional perceptual discrimination deficit or spatial selection bias, we used the Signal Detection Theory to assess changes in perceptual sensitivity index (dprime) and response criterion after unilateral reversible dorsal pulvinar inactivation (Lovejoy and Krauzlis, 2010). Dprime measures how well the monkeys discriminate targets from distractors (Eq. 1); z represents z-score. The response criterion indicates the tendency to select a stimulus in a specific hemifield regardless if it is a target or distractor (Eq. 2).

$$\mathrm{d}' = \mathrm{z}(\text{False alarm rate}) - \mathrm{z}(\text{Hit rate}) \quad (1)$$

$$\mathrm{c} = -0.5(\mathrm{z}(\text{Hit rate}) + \mathrm{z}\,(\text{False alarm rate})) \quad (2)$$

The data were analyzed separately for each monkey (M1 and M2), for each difficulty level (yellow and orange distractor), and stimulus type (single, double same, and double different stimuli). To compare the effect of inactivation per hemifield, we calculated the signal detection variables separately for the contralesional and ipsilesional hemifield relative to the side of inactivation (see the details in the Supplementary Information, **Suppl. Figures S2-S4**).

## Statistical analysis

To assess whether the accuracy differs between the three stimulus types (single stimuli, double same, and double different stimuli) for each difficulty level in the control sessions due intended

consequence of our task design, we conducted a mixed ANOVA followed by post-hoc tests to determine whether the three stimulus types differed significantly. The resulting p-values were corrected for multiple comparisons using Bonferroni correction.

The main of the study is to investigate the effects of dorsal pulvinar inactivation compared to a no perturbation on different dependent variables. Accuracy was analyzed with three-way mixed ANOVAs (Difficulty level, Stimulus type, Perturbation). The dprime and criterion were analyzed with four-way mixed ANOVAs (Difficulty level, Stimulus type, Perturbation, Hemifield). Although the four-factor mixed ANOVA includes all possible interactions, it cannot directly answer our research question whether dPul inactivation affects the criterion or dprime, differently for the three stimulus types or the two perceptual difficulty levels. To assess whether there was a statistical difference between the inactivation sessions and control sessions in the dprime and criterion, we conducted independent sample t-tests for the stimulus position (contralesional vs. ipsilesional hemifield), the stimulus type (single, double same, and double different), and the difficulty level.

## Simulations

We numerically simulated different scenarios of stimulus selection corresponding to the two alternative hypotheses. This analysis aimed to visualize the effects of unilateral inactivation on selection behavior and resulting STD variables for each scenario, and to compare the changes derived from the predictions of each hypothesis with the data. One group of scenarios represents the response criterion, where we expect a decrease both in contralesional hit rate and false alarm rate after the inactivation, resulting in a shift of criterion towards “less contra”. The other group of scenarios represents the perceptual discrimination hypothesis, where we expect a decrease in the contralesional hit rate and an increase in false alarm rate, resulting in decreased contralesional dprime. In brief, the proportions of hits, misses, correct rejections, and false alarms were defined for the control condition, approximately based on the actual monkey performance. A specific bias or perceptual deficit on these proportions was introduced to estimate resulting hits, misses, correct rejections, and false alarms in the “inactivated” condition. The resulting criterion and dprime values were calculated for the control and the inactivated conditions.

For each scenario, the simulated data consist of 200 trials (100 target trials and 100 distractor trials) separated into four different outcomes: hits, misses, false alarms and correction rejections. The proportion of selection for one specific stimulus type and one difficulty level is set in each scenario. An example of a specific selection pattern is illustrated for the scenario “single stimulus – difficult distractor – response criterion hypothesis” (**Table 1**). Before inactivation, the (contralateral) selection pattern is: hits: 0.7 fraction of target selection (correct,

70 trials), misses: 0.3 fraction staying when a target is presented (incorrect, 30 trials); correct rejections 0.6 fraction staying when a difficult distractor is presented (correct, 60 trials) and false alarms: 0.4 fraction selecting the distractor (incorrect, 40 trials). The hit rate is 0.7, and the false alarm rate is 0.4 resulting in a criterion of -0.14 and a dprime of 0.8. According to the prediction of response bias hypothesis, after the inactivation the monkey is selecting less often stimuli presented in the contralesional hemifield regardless whether of a target or a distractor is shown; we expect a decrease of hits and false alarms, and an increase of misses and correct rejections, resulting into a decrease of the contralesional hit rate and false alarm rate. We chose an inactivation-induced decrease in contralesional selection by 0.2 (20 trials) for the hit and false alarm rates, respectively. In this the specific scenario, a decrease in false alarm rate and hit rate after inactivation shifts the criterion towards “less contra”. Notably, the dprime is also changing slightly. To visualize how the hit rate, the false alarm rate, the criterion and the dprime are related, we visualized for each combination of the false alarm rate and the hit rate the resulting values of criterion and dprime.

All simulations were done in MATLAB. The code publically is available at https://github.com/dagdpz/perceptual-dis.

Table 1. Selection pattern for the simulated scenario “single stimulus – difficult distractor – response bias hypothesis”.

| | **Before inactivation** | **Inactivation effect** | **After inactivation** |
|---|---|---|---|
| Hits (%) | 0.70 | - 0.2 | 0.50 |
| Misses (%) | 0.30 | + 0.2 | 0.50 |
| Correct rejections (%) | 0.60 | + 0.2 | 0.80 |
| False alarms (%) | 0.40 | - 0.2 | 0.20 |
| Hit rate | 0.70 | - 0.2 | 0.50 |
| False alarm rate | 0.40 | - 0.2 | 0.20 |
| **criterion** | **-0.14** | | **0.42** |
| **dprime** | **0.77** | | **0.84** |

# Results

We investigated whether local unilateral injection of THIP disrupting the dorsal pulvinar neuronal activity (**Figure 1A**) causes a contralesional perceptual discrimination deficit or a spatial selection bias. Two monkeys performed a color discrimination task between red targets and distractors (orange stimuli as difficult distractors and yellow stimuli as easy distractors) in three stimulus type conditions (single stimuli, double same stimuli, double different stimuli, **Figure 1B**). We analyzed the following dependent variables: saccade latency, accuracy, dprime, and response criterion. The main statistical analysis focused on the comparison between control vs. inactivation sessions.

## The effect of dorsal pulvinar inactivation on saccade latency

The saccade latency is a sensitive measure of the effect of dorsal pulvinar inactivation. According to previous work, we expected either faster ipsilesional saccades (Wilke et al. 2010) or/and slower contralesional saccades (Wilke et al. 2013). A three-way mixed ANOVA (see details in **Suppl. Table S1**) was performed to compare the effect of the within-factors "Stimulus Type" (Single / Double Same / Double Different) and "Hemifield" (Contra- / Ipsilateral hemifield) and the between-factor "Perturbation" (Control / Inactivation sessions) on saccade latency. There was a statistically significant Stimulus type × Hemifield × Perturbation interaction for both monkeys (3-way interaction: M1: $F(2,22) = 4.64$, $p = .021$; M2: $F(2,24) = 3.74$, $p = .039$), as well as the Hemifield × Perturbation interaction for M1 (2-way interaction: M1: $F(1,11) = 21.81$, $p = .001$; M2: $F(1,12) = 3.74$, $p = .087$).

In agreement with our expectations about the inactivation effects, both monkeys significantly slowed down after dorsal pulvinar inactivation during contralesional target selection for both difficulty levels in all three stimulus types (independent t-test, **Table 2**, **Figure 2**). The consistent inactivation effect across stimulus types and difficulty levels on the contralesional saccade latency indicated a successful pharmacological manipulation. The saccade latency effects for ipsilesional target selection were less pronounced and only reached significance for the double same stimuli (independent t-test, **Table 2**, **Figure 2)**.

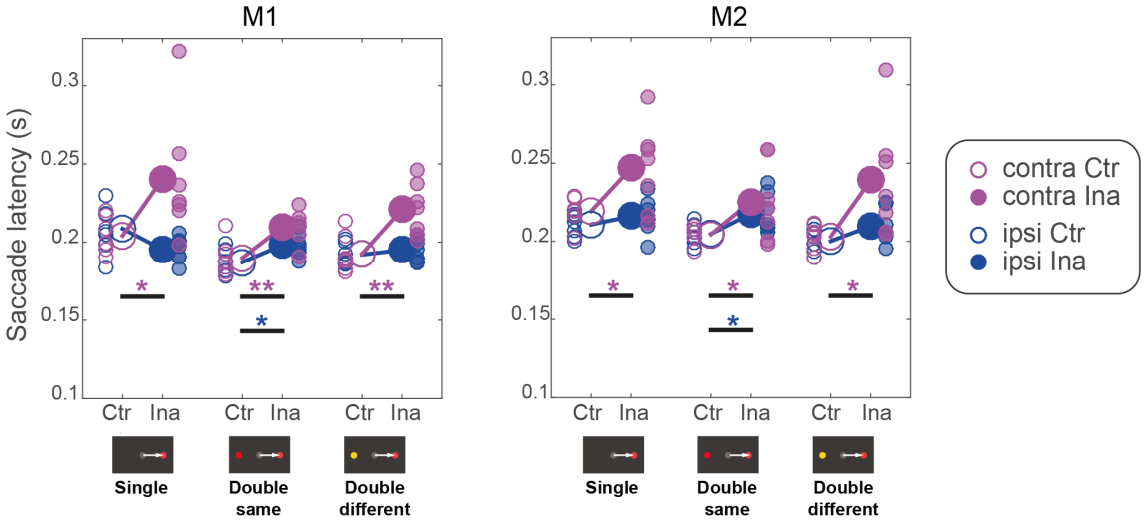


**Figure 2.** Inactivation effects on saccade latency to the target. The saccade latency is displayed separately for control (empty circles, "Ctr") and inactivation (filled circles, "Ina") sessions for each stimulus type and hemifield (icons below horizontal axis show example stimulus display for one hemifield). Small circles display single sessions; large circles display the mean across sessions. We tested the difference between control and inactivation saccade latency of selecting either contralesional (magenta) or ipsilesional (blue) stimuli (independent t-test, one star *, $p < .05$; two stars **, $p<0.01$).

**Table 2.** Results of the independent t-test for the saccade latency after the inactivation. The significant effects are in bold font.

| Stimulus type | Hemifield | Monkey 1 (M1) | | Monkey 2 (M2) | |
|---|---|---|---|---|---|
| | | t-value | p-value | t-value | p-value |
| Single stimuli | **contra** | **2.31** | **.039** | **2.47** | **.029** |
| | ipsi | 2.07 | .061 | 0.99 | .342 |
| Double same stimuli | **contra** | **3.21** | **.008** | **2.19** | **.049** |
| | **ipsi** | **2.81** | **.016** | **2.43** | **.032** |
| Double different stimuli | **contra** | **3.62** | **.004** | **2.54** | **.026** |
| | ipsi | 0.80 | .44 | 1.91 | .081 |

## The effect of inactivation on accuracy

In the control sessions, the difference between accuracy for easy vs difficult discrimination was the intended consequence of our task design. However, when analyzed separately within each difficulty level, we also observed a difference between the three stimulus types (repeated measures one-way ANOVA, within-factor “Stimulus Type”; for difficult discrimination: monkey M1: $F(2,20) = 132.26$, $p < .001$; monkey M2: $F(2,20) = 115.96$, $p < .001$; but not for the easy discrimination: M1: $F(2,20) = 2.23$, $p = .15$; M2: $F(2,20) = 2.54$, $p = .12$). In both monkeys, the accuracy was highest for the double different stimuli and lowest in the double same stimuli for the difficult distractor (post-hoc tests; **Suppl. Table S2**). This difference in accuracy suggests that the three stimulus types elicited different behavioral strategies (for instance, direct comparison between hemifields for double different stimuli vs. only memorized representations of targets and distractors in double same and single stimuli; see later).

We next analyzed the effects of inactivation on accuracy using a three-way mixed ANOVA with within-factors “Stimulus Type” (Single / Double Same / Double Different) and “Difficulty” (Difficult / Easy discrimination) and between-factor “Perturbation” (Control / Inactivation sessions). This analysis (see details in **Suppl. Table S3**) revealed that there was no main effect of the factor “Perturbation” and no statistically significant interactions with this factor for M1. However, the main effect of the “Perturbation” and the two-way interaction between Stimulus Type × Experiment was significant for M2 ($F(1,12) = 9.4$, $p = .01$, $F(2,24) = 6.4$, $p = .006$).

The results for M2 were followed up to investigate the effect of inactivation by applying post-hoc tests. M2 showed a significant decrease in accuracy for single stimuli for the easy distractor ($t(1,12) = -2.26$, $p = .04$) and for double different stimuli for both difficulty levels (difficult: $t(1,12) = -2.67$, $p = .02$; easy: $t(1,12) = -3.73$, $p = .003$) but not for double same stimuli (difficult: $t(1,12) = 0.18$, $p = .86$; easy: $t(1,12) = 1.48$, $p = .16$) or difficult single stimuli ($t(1,12)$

= 0.86, p = .4) (**Figure 3**). These effects will be addressed with the Signal Detection Theory analysis below.

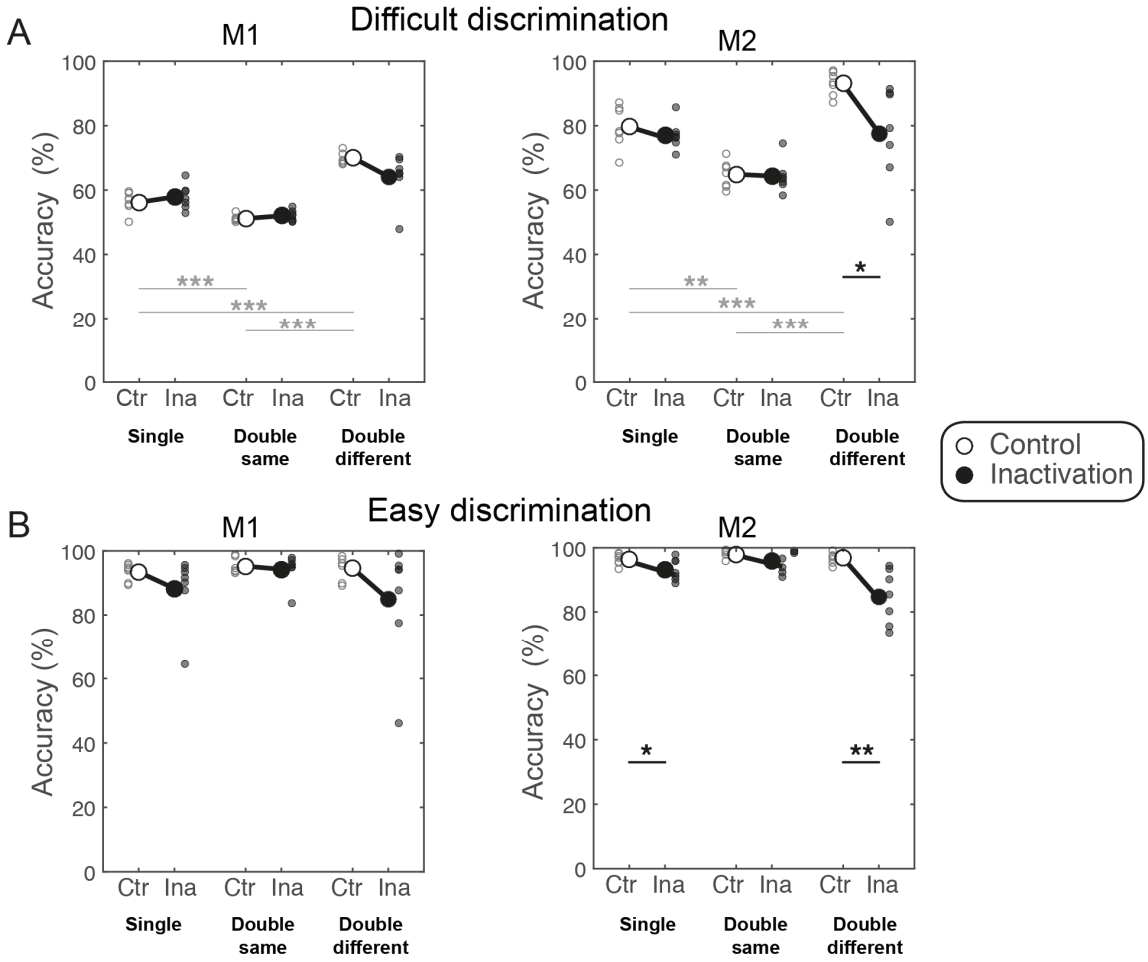


**Figure 3.** Inactivation effects on accuracy. The accuracy is displayed separately for control (Ctr) and inactivation (Ina) sessions for each stimulus type and difficulty level. Small circles depict single sessions, and large circles indicate the mean across sessions. Two statistical analyses are presented: the difference between control and inactivation sessions (black connecting lines and stars) and the difference in accuracy between stimulus types (single, double same, double different) for the control sessions (gray connecting lines and stars). (A) Difficult discrimination. The inactivation did not affect the accuracy, besides a decrease in the double different condition in M2. Considering only the control sessions per stimulus type, the accuracy significantly varied between stimulus types. (B) Easy discrimination. The inactivation affected accuracy for M2 for single and double different conditions. The accuracy in the control condition was very high and did not vary between stimulus types. Independent t-test, one star *, p < .05; two stars **, p<0.01; three stars ***, p<0.001.

## The effect of inactivation on criterion and dprime

We adopted the Signal Detection Theory approach to differentiate between the spatial selection bias by calculating the response criterion and the deficit in perceptual discrimination between stimuli by calculating dprime. To assess at first all possible interaction effects on

criterion and dprime, a four-factor mixed ANOVA was used per monkey including as within-factors “Stimulus Type” (Single / Double Same / Double different), “Difficulty” (Difficult / Easy discrimination) and “Hemifield” (Contra- / Ipsilesional) and as between-factor “Perturbation” (Control / Inactivation sessions). Most important, the mixed ANOVA revealed that there was a significant interaction of all four factors (Stimulus Type × Difficulty × Hemifield × Perturbation) for M1 for the criterion ($F(2,24) = 8.69$, $p = .001$) and dprime ($F(2,24) = 3.87$, $p = .035$) but not for M2 (criterion: $F(2,24) = 0.74$, $p = .49$, dprime: $F(2,24) = 0.33$, $p = .72$). Instead, M2 showed a significant three-way Perturbation × Stimulus Type × Hemifield interaction ($F(2,24) = 7.82$, $p = .002$) for the criterion and a significant two-way Stimulus Type × Perturbation interaction ($F(2,24) = 8.76$, $p = .001$) for the dprime (see the details in the in **Suppl. Table S4**).

Although the four-factor mixed ANOVA includes all possible interactions, it cannot directly answer our research question such as whether dPul inactivation affects the criterion or dprime, differently for the three stimulus types or the two perceptual difficulty levels. In both monkeys, we observed interactions of the factors “Perturbation” and “Hemifield”, and we had hemifield-specific predictions. To test these predictions, we continue the analysis of dprime and criterion focusing on a 2-factor mixed ANOVA with within-factor “Hemifield” (Contra- / Ipsilesional) and between-factor “Perturbation” (Control / Inactivation sessions), and the corresponding post-hoc t-tests, separately for each stimulus type and difficulty.

## The effect of inactivation for single stimuli

The single stimuli condition involves a perceptual judgment between making a saccade to a peripheral target or continuing fixating as the correct response to a peripheral distractor (low spatial competition between a central “stay” and peripheral “go” options). To evaluate a deficit in discrimination versus a spatial selection bias, we divided trials into hits, misses, correct rejections and false alarms separately for stimuli presented in the contralesional (hemifield opposite to the side of inactivation) or ipsilesional side to calculate the hit rate, false alarm rate, dprime and criterion for each hemifield (**Suppl. Figure S2**). Since we used two different distractors, one easy distractor (yellow) being perceptually clearly different from the red target while the other (orange) requiring a difficult perceptual discrimination, we analyzed these two distractor conditions separately, contrasting them to target trials. Here and in the next sections, we first describe quantitative predictions using simulated data, and then the actual data.

During difficult discrimination, if dorsal pulvinar inactivation causes a spatial selection we expect a similar decrease both in contralesional hit rate and false alarm rate, resulting in a shift of criterion towards “less contra” (**Figure 4A**). If the inactivation causes a contralesional perceptual discrimination deficit we expect a decrease in contralesional hit rate and an

increase in false alarm rate, resulting in decreased contralesional dprime (**Figure 4A**). We did not expect changes to the ipsilesional criterion and dprime.

In the target trials, the contralesional hit rate decreased after the inactivation, significantly for M2 (independent t-test; M1: $t(1,12) = 1.1$, $p = .29$; M2: $t(1,12) = -2.89$, $p = .01$). For difficult discrimination (**Figure 4B**), the contralesional false alarm rate also decreased but this effect did not reach significance (M1: $t(1,12) = 1.15$, $p = .27$; M2: $t(1,12) = 1.6$, $p = .14$). Consequently, neither monkey showed a decrease in contralesional dprime after inactivation (M1: $t(1,12) = -0.36$, $p = .73$; M2: $t(1,12) = -1.26$, $p = .23$). However, one monkey showed a significant shift for the contralesional criterion towards "less contra" (M2: $t(1,12) = 3.07$, $p = .01$; the effect was similar but did not reach significance in M1, $t(1,12) = 1.21$, $p = .25$). In line with our predictions, in both monkeys neither ipsilesional dprime nor the ipsilesional criterion exhibited any changes (dprime M1: $t(1,12) = -0.41$, $p = .69$; M2: $t(1,12) = -1.98$, $p = .07$; criterion M1: $t(1,12) = 0.99$, $p = .34$; M2: $t(1,12) = 0.15$, $p = .89$).

During easy discrimination, if dorsal pulvinar inactivation causes a spatial selection bias we expect a decrease in contralesional hit rate but now no change in false alarm rate due to a "ceiling effect" (already very low false alarm rate in the control sessions). This will result in a shift of criterion towards "less contra" combined with a decrease in contralesional dprime (**Figure 4C**). For completeness, if the inactivation causes a contralesional perceptual discrimination deficit one expects a decrease in contralesional hit rate and an increase in false alarm rate (although given the easy discriminability of the yellow distractor, we did not expect such increase in the actual behavior). This would result in decreased contralesional dprime but no change in criterion (**Figure 4C**).

Indeed, in both monkeys during easy discrimination (**Figure 4D**), the false alarm rate was already near zero, so there was no room to exhibit any inactivation-induced decrease (independent t-test; contra M1: $t(1,12) = 0.02$, $p = .98$; M2: $t(1,12) = -0.3$, $p = .7$; ipsi M1: $t(1,12) = 0.95$, $p = .36$; M2: $t(1,12) = -0.6$, $p = .6$). One monkey (M2) showed a significant shift for the contralesional criterion towards "less contra" (M1: $t(1,12) = 0.85$, $p = .41$; M2: $t(1,12) = 2.63$, $p = .02$), but also a decrease in contralesional dprime (M1: $t(1,12) = -1.49$, $p = .16$; M2: $t(1,12) = 2.27$, $p = .04$). This decrease in dprime was due to the "ceiling effect" of already very low false alarm rate, as predicted in the simulation.

Thus, under conditions of low spatial competition, both monkeys showed a shift in response criterion after inactivation manifesting as reluctance to select stimuli in the contralesional hemifield for both difficulty levels, significant in monkey M2.

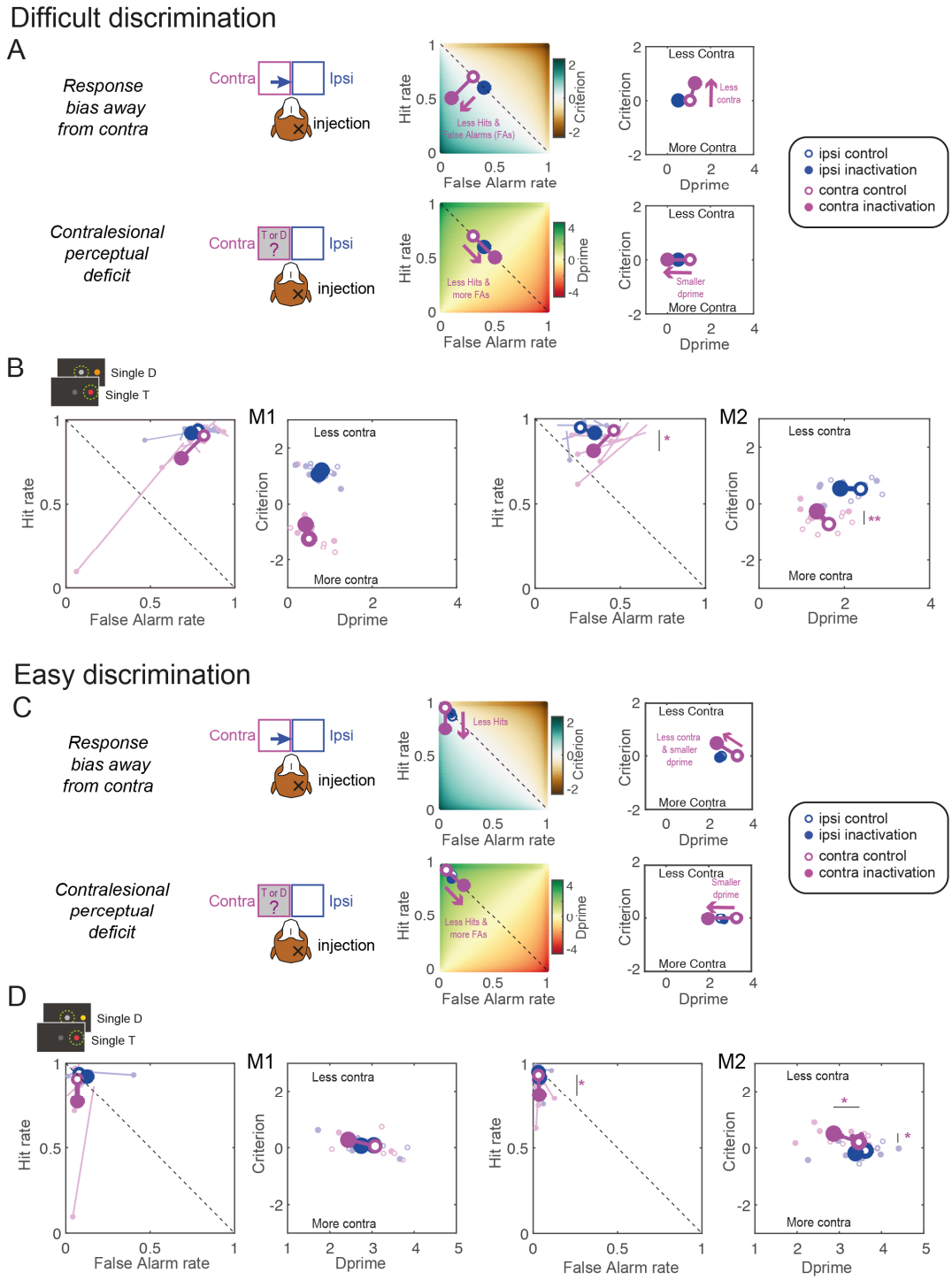


**Figure 4.** Predictions and results for single stimuli. (A) Illustration of the two alternative hypotheses for the difficult discrimination using simulated data showing the expected changes in hit rate, false alarm rate, dprime and criterion after unilateral dPul inactivation. (B) Inactivation effects on signal detection variables for the difficult discrimination (orange distractor); the data are displayed separately for each monkey: the left panel shows the ipsilesional (blue) and contralesional (magenta) false alarm rate and hit rate, the right panel shows the ipsilesional and contralesional criterion and dprime. Small circles display single sessions; large circles display the mean across sessions. (C) Illustration of the two alternative hypotheses for the easy discrimination. (D) Inactivation effects on signal detection variables for the easy discrimination (yellow distractor). Abbreviations: T – target, D – distractor, Contra – contralesional, ipsi – ipsilesional.

## The effect of inactivation for double same stimuli

Previous studies suggested that dorsal pulvinar becomes most relevant in the case of spatial competition between hemifields (Desimone et al., 1990; Wilke et al., 2013; Dominguez-Vargas et al., 2017). Here, two equally rewarded targets or two distractors were presented in the periphery during the same stimuli condition, eliciting a high competition between hemifields for visual representation and response selection. The monkeys chose between continuing fixating or making a saccade to one of the two peripheral stimuli (**Suppl. Figure 3**).

As for the single stimuli, if dorsal pulvinar inactivation causes a spatial selection bias during inter-hemifield competition, we expect a similar decrease in a contralesional hit and false alarm rates. Necessarily, such a decrease has to result in (i) a corresponding increase in ipsilesional hit rate and false alarm rate, or (ii) an increase of central fixation selection. Both monkeys tended to select peripheral stimuli, even after inactivation, based on a non-hemifield-selective criterion analysis ("stay" vs. "go", **Suppl. Table 7**). Therefore, we expected a shift for both contralesional and ipsilesional criteria towards "less contra" (**Figure 5A**). If dorsal pulvinar inactivation causes a contralesional perceptual discrimination deficit, we expect a decrease in contralesional hit rate and an increase in contralesional false alarm rate resulting in a reduction of contralesional dprime (**Figure 5A**). We did not have strong predictions for the ipsilesional discrimination: it might remain unaffected, as for single stimuli (instead, only fixation responses will be affected), or it might improve as a consequence of ipsilesional hit rate increase and ipsilesional false alarm rate decrease. For simplicity, we assumed no change for the ipsilesional discrimination.

The contralesional hit rate decreased significantly for both monkeys (independent t-test; M1: $t(1,12) = -4.24$, $p < .001$; M2: $t(1,12) = -4.78$, $p < .001$), and ipsilesional hit rate increased significantly (M1: $t(1,12) = 4.36$, $p < .001$; M2: $t(1,12) = 3.28$, $p = .01$). For difficult discrimination displayed in **Figure 5B**, the ipsilesional false alarm rate significantly increased for both monkeys (M1: $t(1,12) = 3.25$, $p = .01$; M2: $t(1,12) = 3.23$, $p = .01$) and contralesional false alarm rate significantly decreased for M1 (M1: $t(1,12) = -2.79$, $p = .02$; M2: $t(1,12) = -2.04$, $p < .065$). Both monkeys showed a significant shift for the contralesional and ipsilesional criterion towards "less contra" (M1 contra: $t(1,12) = 2.68$, $p = .02$, ipsi: $t(1,12) = 3.74$, $p = .003$; M2 contra: $t(1,12) = 2.87$, $p =.014$, ipsi: $t(1,12) = -3.8$, $p = .003$). Neither monkey showed a significant change in contralesional dprime ($p > .05$).

During easy discrimination, as for the single stimuli, for the spatial selection bias hypothesis we expect a decrease in contralesional hit rate and no observable decrease in false alarm rate (again due to ceiling effect on already very low false alarm rate), and a corresponding increase in ipsilesional hit rate, but no increase in false alarm rate, due to easy discriminability of the

distractor. These changes should result in a shift for both criteria towards “less contra” combined with a change in dprime values (**Figure 5C**). For the contralesional perceptual discrimination deficit hypothesis, we expect a decrease in contralesional hit rate and an increase in false alarm rate resulting in a decrease in contralesional dprime (**Figure 5C**).

For easy discrimination (**Figure 5D**), the false alarm rate was already near zero, so there was no room to exhibit any inactivation-induced decrease that was expected according to the spatial selection bias hypothesis. Hence, the contralesional false alarm rate did not show an effect (independent t-test; M1: $t(1,12) = -0.94$, $p = .2$; M2: $t(1,12) = 1.82$, $p = .09$). The ipsilesional false alarm rate slightly increased, significant for one monkey (M1: $t(1,12) = 1.37$, $p =0.37$; M2: $t(1,12) = 2.32$, $p= .04$). Consequently, both monkeys showed a significant shift for the contralesional and ipsilesional criterion towards “less contra” (M1 contra: $t(1,12) = 2.83$, $p = .015$, ipsi: $t(1,12) = 2.66$, $p = .021$; M2 contra: $t(1,12) = 3.6$, $p = .004$, ipsi: $t(1,12) = 7.66$, $p < .001$). Both monkeys also showed a significant decrease in contralesional dprime (M1: $t(1,12) = -2.32$, $p = .039$; M2: $t(1,12) = -2.30$, $p = .04$), due to the already very low false alarm rate, and M1 showed an increase in ipsilesional dprime (M1: $(1,12) = 3.31$, $p = .006$, M2: $(1,12) = -0.38$, $p = .71$), due to increase in ipsilesional hit rate but without corresponding increase in ipsilesional false alarm rate. All in all, the data are much more consistent with the spatial selection bias hypothesis.

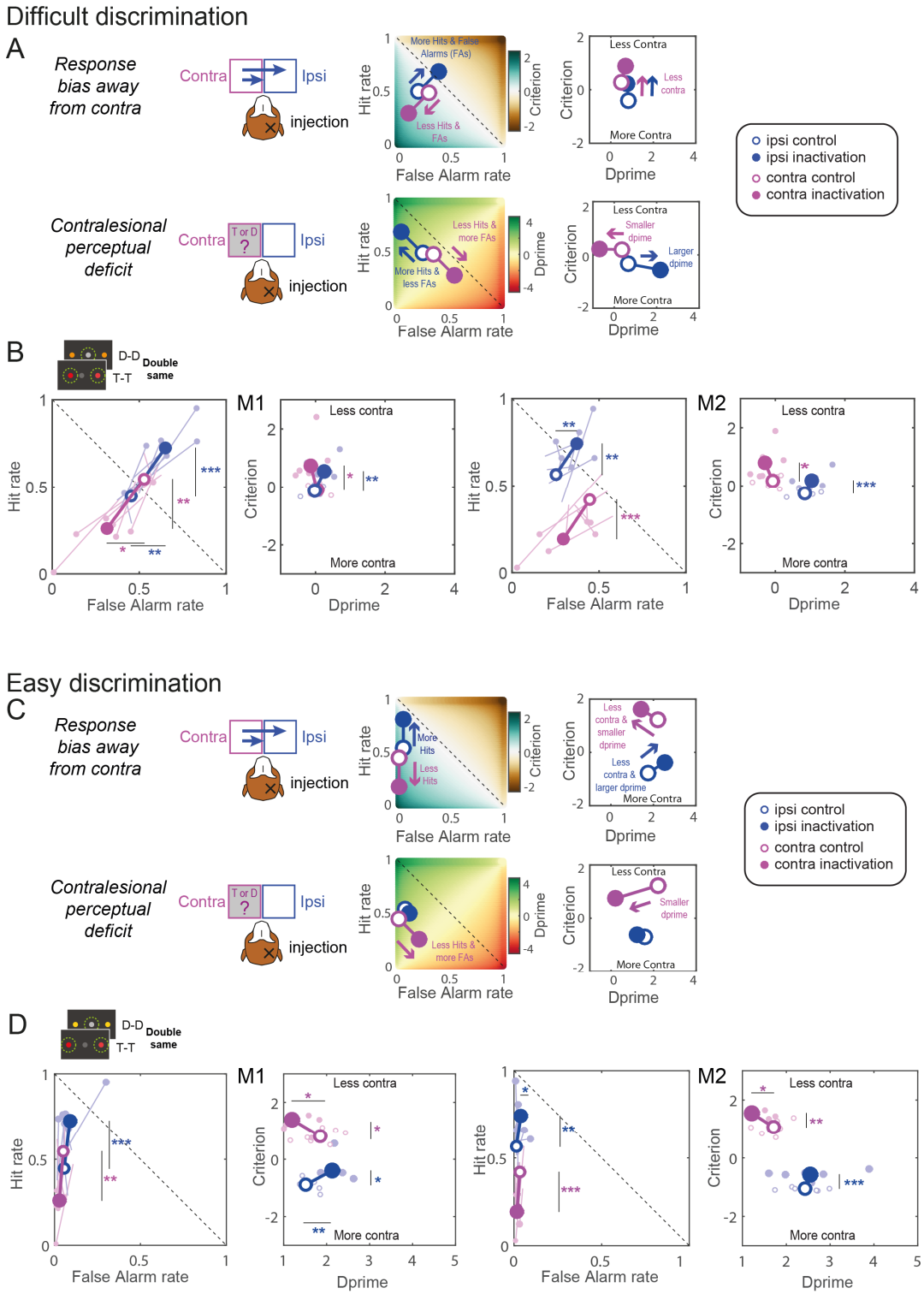


**Figure 5.** Predictions and results for double same stimuli. Same format and notations as in Figure 4.

## The effect of inactivation for double different stimuli

The double different stimuli condition also includes a high spatial competition between hemifields. Furthermore, it is influenced by the possibility of directly comparing the simultaneously presented target and distractor in the opposite hemifields. Notably, the central fixation is always an incorrect response option (**Suppl. Figure 4**).

During difficult discrimination, for the spatial selection bias hypothesis we expect the same effect as in the double same stimuli (**Figure 6A**). But for the discrimination deficit hypothesis, in contrast to double same stimuli, assuming the "go" bias, here we expect the decrease in contralesional dprime to be necessarily linked to the *decrease* in ipsilesional dprime, because selecting less targets on contralesional side would lead to selecting more distractors in the ipsilesional side, and selecting more contralesional distractors – to less ipsilesional targets (**Figure 6A**). The contralesional hit rate decreased significantly (independent t-test; M1: $t(1,12) = -2.8$, $p = .02$; M2: $t(1,12) = -2.98$ $p = .01$) and ipsilesional hit rate increased for M1 (M1: $t(1,12)= 2.92$, $p = .01$; M2: $t(1,12) = 1.49$, $p = .16$; **Figure 6B**). The contralesional and ipsilesional false alarm rate significantly decreased only for M1 (contra: M1: $t(1,12) = -2.9$, $p = .01$; M2: $t(1,12) = -0.65$, $p = .53$; ipsi: M1: $t(1,12) = -2.9$, $p = .01$; M2: $t(1,12) = -1.8$, $p = .09$). Consequently, M1 showed a significant shift for the contralesional and ipsilesional criterion towards "less contra" (M1 contra: $t(1,12) = 2.4$, $p = .03$, ipsi: $t(1,12) = 2.72$, $p = .02$) and no effect for in contralesional or ipsilesional dprime (contra: $t(1,12) = 1.42$, M1: $p = .18$, $t(1,12) = -2.03$, ipsi: $p = .06$). Likewise, M2 showed a significant shift for the contralesional criterion towards "less contra" (M2: $t(1,12) = 2.42$, $p = .03$) but also a significant decrease in contralesional and ipsilesional dprime (contra: $t(1,12) = -3.14$, $p = .01$; ipsi: $t(1,12) = -3.32$, $p = .006$).

During easy discrimination in the presence of a yellow distractor, for the spatial selection bias hypothesis, we expect a decrease in a contralesional hit without the decrease in false alarm rate due to the "ceiling effect". We expect no increase in the ipsilesional hit rate because it is already very high and no increase in the ipsilesional false alarm rate because of the easy discriminability of the yellow distractor (**Figure 6C**). For contralesional perceptual discrimination deficit, similarly to the double same stimuli, we expect a decrease in contralesional dprime but no effect on ipsilesional dprime (**Figure 6C**).

For easy discrimination (**Figure 6D**), the false alarm rate was already near zero, so there was no room to exhibit any inactivation-induced decrease. Hence, the contralesional false alarm rate did not show an effect, while ipsilesional false alarm rate did not increase (independent t-test; contra: M1: $t(1,12) = 0.8$, $p = .47$; M2: $t(1,12) = -1.87$, $p = .09$; ipsi: M1: $t(1,12) = -0.98$, $p = .35$; M2: $t(1,12) = -1.66$, $p = .12$). The contralesional hit rate decreased for M2 (M1: $t(1,12) =$

1.2, $p = .25$; M2: $t(1,12) = -2.9$, $p < .001$). One monkey (M2) showed a significant shift for the contralesional criterion towards “less contra” (M1: $t(1,12) = 0.82$, $p = .25$, M2: $t(1,12) = 4.75$, $p < .001$) and a significant decrease in contralesional and ipsilesional dprime (contra M1: $t(1,12) = -0.82$, $p = .43$, M2: $t(1,12) = -5.16$, $p < .001$; ipsi: M1: $t(1,12) = -2.03$, $p = .07$, M2: $t(1,12) = 2.19$, $p = .05$). This decrease in dprime was due to the “ceiling effect” of already very low false alarm rate.

To sum up, the results for M1 during difficult discrimination matched the predictions of the spatial selection bias hypothesis (shift of both contralesional and ipsilesional criteria towards less contra). In contrast, in M2, only the contralesional criterion, for both difficulty levels, shifted towards less contra. For M2, we also observed a decrease in contralesional dprime for both difficulty levels and a decrease in ipsilesional dprime for the difficult discrimination. The contralesional dprime decline can be accounted for by the “ceiling effect” on the already very low false alarm rate (for both difficulty levels), as in the single stimuli and double same stimuli conditions for easy discrimination. But the ipsilesional dprime decrease, which only manifested in the double different stimuli condition, can be related to the compromised ability of this monkey to utilize the information from the contralesional hemifield for the direct comparison with the ipsilesional stimulus – the strategy that the monkey successfully relied on the control sessions (*cf.* **Figure 3**). We further address this hypothesis in the Discussion.

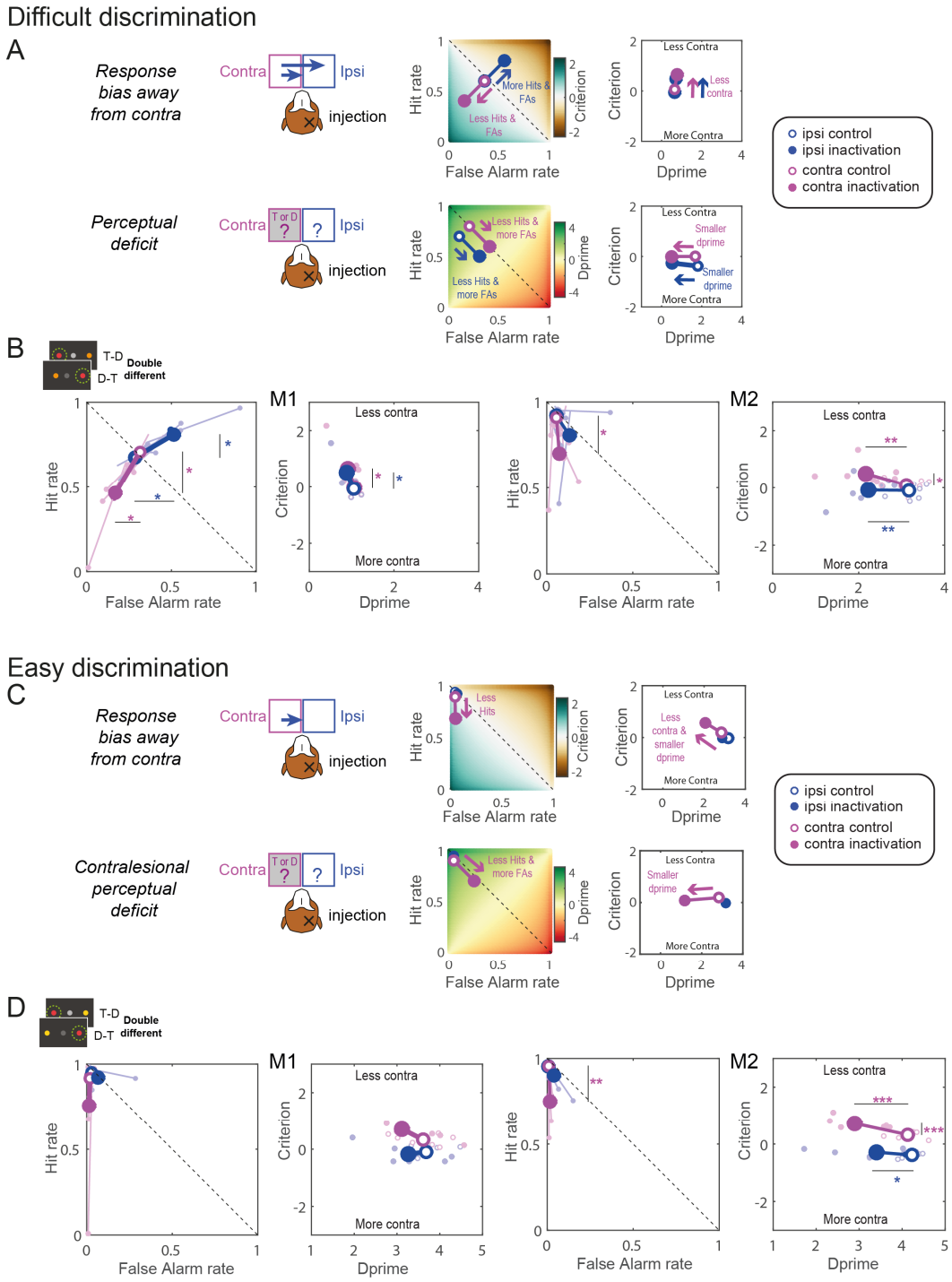


**Figure 6.** Predictions and results for double different stimuli. Same format and notations as in Figure 4.

**Table 3.** Summary of inactivation effects for the criterion and dprime using independent t-tests. Significant effects are in bold font, consistent effects across the two monkeys are highlighted with gray background. **Suppl. Figures S5** and **S6** plot the corresponding data.

| Stimulus type | Difficulty | Measure | Hemifield | Monkey 1 | | | Monkey 2 | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | t-value | p-value | Direction of the effect | t-value | p-value | Direction of the effect |
| Single stimuli | difficult | criterion | contra | 1.21 | .25 | - | **3.07** | **.01** | **Less contra** |
| | | | ipsi | 0.99 | .34 | - | -0.15 | .88 | - |
| | | dprime | contra | -0.36 | .73 | - | -1.26 | .23 | - |
| | | | ipsi | -0.41 | .69 | - | -1.98 | .07 | - |
| | easy | criterion | contra | 0.85 | .41 | - | **2.63** | **.02** | **Less contra** |
| | | | ipsi | 0.12 | .91 | - | 0.74 | .47 | - |
| | | dprime | contra | -1.49 | .16 | - | **-2.27** | **.04** | **Decrease** |
| | | | ipsi | -1.08 | .30 | - | -0.83 | .42 | - |
| Double same stimuli | difficult | **criterion** | **contra** | **2.68** | **.02** | **Less contra** | **2.87** | **.01** | **Less contra** |
| | | | **ipsi** | **-3.74** | **.003** | **Less contra** | **-3.80** | **.003** | **Less contra** |
| | | dprime | contra | -1.28 | .23 | - | -1.39 | .18 | - |
| | | | ipsi | 1.89 | .08 | - | 1.04 | .32 | - |
| | easy | **criterion** | **contra** | **2.83** | **.02** | **Less contra** | **3.60** | **.004** | **Less contra** |
| | | | **ipsi** | **-2.66** | **.02** | **Less contra** | **7.66** | **.001** | **Less contra** |
| | | **dprime** | **contra** | **-2.32** | **.04** | **Decrease** | **-2.30** | **.04** | **Decrease** |
| | | | **ipsi** | **3.31** | **.006** | **Increase** | 0.38 | .71 | - |
| Double different stimuli | difficult | **criterion** | **contra** | **2.40** | **.03** | **Less contra** | **2.42** | **.03** | **Less contra** |
| | | | ipsi | -2.72 | .02 | Less contra | -0.07 | .95 | - |
| | | dprime | contra | -1.42 | .18 | - | **-3.14** | **.009** | **Decrease** |
| | | | ipsi | -2.03 | .07 | - | **-3.32** | **.006** | **Decrease** |
| | easy | criterion | contra | 1.20 | .25 | - | **4.75** | **.001** | **Less contra** |
| | | | ipsi | 0.58 | .57 | - | -1.84 | .09 | - |
| | | dprime | contra | -0.82 | .43 | - | **-5.16** | **.001** | **Decrease** |
| | | | ipsi | -1.23 | .24 | - | **-2.19** | **.049** | **Decrease** |

# Discussion

This study used task demands such as fast perceptual color discrimination between target and distractor, spatially competing stimuli, and stimulus-congruent saccade responses to investigate whether the impairments in contralesional perceptual discrimination might contribute to visuospatial deficits after dorsal pulvinar inactivation. Following the inactivation, we primarily observed slowing of contralesional saccades and criterion shifts away from contralesional stimuli, especially when two peripheral stimuli elicited high spatial competition between hemifields (**Table 3**). These effects were present at both difficulty levels. Notably, the dprime and the overall accuracy remained largely unaffected. We conclude that the contralesional visuospatial deficits observed after inactivating the dorsal pulvinar are not caused by a contralesional perceptual deficiency but by a spatial selection bias.

We adopted the Signal Detection Theory approach to differentiate between the spatial selection bias by calculating the response criterion and the discrimination between stimuli by calculating dprime (Luo and Maunsell, 2015). After inactivation, a shift in criterion manifested as reluctance to select stimuli in the contralesional hemifield, regardless of whether a target or

distractor was presented there. This spatial selection bias and delays in making a saccade to contralesional stimuli were observed for all three stimulus conditions (single, double same, and double different). As in our previous studies, (Wilke et al., 2010, 2013), we found a pronounced selection bias “away from contra” for the double same stimulus condition most similar to the free-choice between two identical targets. For single stimuli, the shift of the criterion “away from contra” was significant for one monkey and similar but not significant for the other monkey.

In contrast, Wilke et al. (2010, 2013) did not find a decrease in the correct selection of contralesional single instructed targets. Their instructed condition differed from our single stimulus condition because monkeys invariably had to saccade to the target. Here we included a second response option, central fixation, as the correct response for the distractor trials. The presence of two options and the perceptual discrimination context created a low spatial competition between the fixation option and peripheral option for single stimuli. Hence, the dorsal pulvinar inactivation influences the competition between the hemifields and also the competition between the foveal and the contralesional options. During action selection, multiple response options compete against each other. At the same time, information is collected to bias this competition between representations at different levels of neuronal processing until one option is selected (Cisek, 2006). Our findings show that the dorsal pulvinar is involved in biasing such spatial competition during perceptual decisions, likely via its extensive connectivity to the frontoparietal cortical network in the same hemisphere.

Support for the importance of spatial competition also comes from a (single) monkey study by Desimone et al. (1990), which inactivated lateral pulvinar during a color rule task that required responding with a lever to a briefly flashed colored target and not to a distractor. The target was defined as the stimulus appearing at the same location as the briefly flashed cue. The error rate increased when the cue and the target were in contralesional hemifield while the conflicting distractor was in the ipsilesional hemifield. When both the target and the distractor were in the same visual field leading to no spatial competition between hemifields, no significant effect of pulvinar inactivation on performance was observed.

Notably, the inactivation-induced selection bias occurs even in the context where only one response option is correct and rewarded. Presenting a target in the contralesional hemifield when it is the only rewarded option (single target or target-distractor conditions) did not alleviate the spatial selection bias “away from contra”. Both monkeys selected the contralesional target less and instead chose the ipsilesional distractor or fixation option, receiving no reward in these trials. Again, this contrasts with the observed alleviation of the selection bias in the memory saccade task where a color cue explicitly and unambiguously signaled a large reward, and a memory delay could be used for making a deliberate value-based choice (Wilke et al., 2013). The present results emphasize the contribution of dPul to

fast decisions between conflicting options under uncertainty, in agreement with the previous inactivation study in the lateral pulvinar (Desimone et al., 1990).

A hypothetical inactivation-induced contralesional perceptual discrimination deficit should lead to confusion between targets and distractors in the contralesional hemifield, leading to an increase in false alarm rate combined with a decrease in hit rate and resulting in decreased contralesional dprime. After inactivation, we did not observe a pattern that would be consistent with contralesional perceptual discrimination deficit in any of the three stimulus type conditions (single, double same, and double different). Previous pulvinar lesion studies in non-human primates showed unimpaired visual discrimination learning (Ungerleider and Christensen, 1977; Bender and Butter, 1987) and unimpaired contralesional visual motion discrimination performance without spatially-competing distractors (Komura et al., 2013). These studies used manual responses that were spatially dissociated from the visual stimuli. Our study extends these findings to situations where saccadic responses are spatially-contingent on the stimuli and with competition between spatial locations. Even under these conditions, where the contribution of the pulvinar can be more crucial, the perceptual sensitivity was largely unaffected after pulvinar inactivation.

One possible strategy to accurately discriminate targets from distractors is to compare the currently visible stimuli with a learned and memorized representation of the target and the distractors. These strategies could be used for all three stimulus types. For the double different condition, however, an additional strategy could be used. The visual appearance of the two stimuli, one target, and another distractor, could be directly compared across hemifields without relying on memorized representations. Indeed, in both monkeys, the target-distractor condition had significantly higher accuracy than the single or double same stimuli conditions for the difficult distractor. Furthermore, the accuracy for easy and difficult target-distractor trials was very high and did not significantly differ during control sessions for M2. Hence, the strategy based on direct comparison improved discrimination performance for the target-distractor condition.

After dorsal pulvinar inactivation, M2 accuracy decreased substantially for the difficult target-distractor condition, driven by a significant drop in both, contralesional and ipsilesional dprime. We argue that this is not an indication of a specific contralesional perceptual discrimination deficit but a consequence of a direct across-hemifield comparison strategy, and its partial failure. In this interpretation, M2 avoided going to the contralesional hemifield (due to the criterion shift), but still could utilize the information from the ipsilateral hemifield to correctly reject contralesional distractors, as demonstrated by a very low contralesional false alarm rate even after the inactivation. The resulting contralesional sensitivity decrease is thus similar to the case of easy discrimination but the ipsilesional hit rate did not increase (on the contrary, it

decreased non-significantly). Instead, the contralesional hit rate decrease was compensated by more central fixations. Furthermore, the ipsilesional false alarm rate increased non-significantly. We suggest that the ipsilesional sensitivity decreased because the inactivation disrupted the comparison of information from contralesional hemifield for comparing it to the stimulus in the ipsilesional hemifield.

An ipsilesional selection bias (i.e. away from contra) and/or increased contralesional saccade latencies also occur after inactivating parietal area LIP in a visual search task (Wardak et al., 2002, 2004), or memory saccade task (Li et al., 1999; Wilke et al., 2012), and as well as after inactivating FEF in a visual search task (Wardak et al., 2006). This is in line with dorsal pulvinar reciprocal anatomical (Blatt et al., 1990; Hardy and Lynch, 1992; Romanski et al., 1997; Gutierrez et al., 2000) and functional connections (Arcaro et al., 2018; Fiebelkorn et al., 2019; Kagan et al., 2021) with the frontoparietal cortex. Of course, the specifics of impairments might differ between the regions and the paradigms. For instance, the reaction time deficits in visual search target detection depend on the perceptual task difficulty after LIP but not after FEF inactivation (Wardak et al., 2006). Similarly, the saccade latency increases after the inactivation, suggesting that the inactivation did not impair the perceptual discrimination.

Pulvinar lesions in humans (Karnath et al., 2002; Arend et al., 2008a; Snow et al., 2009) and monkeys (Robinson et al., 1986; Bender and Butter, 1987; Petersen et al., 1987; Desimone et al., 1990; Robinson and Petersen, 1992) lead to spatial deficits in covert attention tasks. These studies raise the possibility of explaining our findings by visual-spatial attention. Experiments investigating spatial attention typically use a valid or invalid cue to signal where to attend to an upcoming target without making an eye movement (Posner et al., 1980; Petersen et al., 1987; Lovejoy and Krauzlis, 2010). Our task was not designed to investigate covert spatial attentional processes or shifts of attention because no cue directed attention before the stimulus onset. Nevertheless, our main finding of the spatial selection bias after dorsal pulvinar inactivation fit well with previous work emphasizing that inactivation of the pulvinar affects both covert and overt spatial selection.

Desimone & Duncan (1995) proposed interpreting the findings after unilateral pulvinar inactivation as formulated in the biased competition theory. In this theory, unilateral dorsal pulvinar inactivation puts the contralesional hemifield at a disadvantage for selection by biasing the ongoing competition for the neuronal representation of multiple stimuli, and leading to the observed bias “away from contra”. They claim that pulvinar resolves the competition for the neural representation of multiple stimuli by two proposed neural mechanisms enhancing target representations and filtering out distracting stimuli. So, neural representations of multiple stimuli also compete for attention. When various stimuli compete for attention, attending to one option biases the competition by enhancing the neuronal activity representing this response

option within their receptive field. Selective attention can bias the competition via bottom-up and top-down mechanisms (Beck and Kastner, 2009; Markowitz et al., 2011).

As selective spatial attention can also be defined through its effect on visual perception, spatial attention facilitates perception at attended stimulus location (Reynolds and Chelazzi, 2004; Carrasco, 2011). Indeed, behavioral responses to attended stimuli are faster and more accurate, and visual selectivity at attended locations is enhanced. Hence, to some extent, visual attention guides perceptual discrimination, stimulus selection, and motor planning in the color discrimination task even though this task did not control for visuospatial attention. Specifically, suppose dorsal pulvinar neurons encode information about the saliency of a target to guide selection. In that case, we expect a decrease in the saliency of the contralesional stimuli after inactivation, leading to (1) contralesional perceptual deficit in discriminating between distractor and the less salient target or/and (2) a decrease in contralesional confidence in choosing the correct response (Fetsch et al., 2014). We found no contralesional perceptual discrimination deficit, and our task did not involve confidence judgments. However, decreasing contralesional confidence in choosing the correct response might lead to a spatial selection bias 'away from contra'. Conversely, the decreased confidence about contralesional stimuli operationalized as the increased frequency of opt-out choices (Komura et al., 2013) may be a consequence of our observed criterion change.

Further studies need to investigate if the spatial selection bias is a consequence of either bottom-up or/and top-down saliency of a stimulus or confidence or their relationship to each other. The ventral pulvinar is also associated with visual attention (Zhou et al., 2016). It can be considered a more perceptually-relevant visual nucleus with extensive connectivity to the primary visual cortex and the ventral visual stream. Given its connectivity, visual response properties, and the findings of a strong perceptual modulation in both ventral and dorsal pulvinar in Wilke et al., 2009, it would be interesting to investigate if the ventral pulvinar inactivation shows a more substantial perceptual deficit than the dorsal pulvinar.

Finally, the function of the pulvinar is often described as distractor filtering (Fischer and Whitney, 2012; Lucas et al., 2019). For instance, LaBerge and Buchsbaum (1990) investigated the pulvinar role in visual distractor processing using positron emission tomography in healthy subjects. Increased pulvinar activation was found when the target in the contralateral visual field was surrounded by distractors relative to no distractors. The authors concluded that identifying an object in a cluttered visual scene may involve the pulvinar through a filtering mechanism. Several fMRI studies also showed increased activation during more demanding distractor conditions – but these effects could have been driven by task difficulty and response competition rather than specific contralateral filtering processing (Kastner et al., 2004; Strumpf et al., 2013). The hypothesis that the pulvinar participates in filtering distracting visuospatial

inputs in the contralateral hemifield was also advocated in a patient study by Van der Stigchel, Arend, van Koningsbruggen, and Rafal (2010) – although the effect was very small (3% error rate), and another patient study in ventral pulvinar showing impaired contralateral perceptual discrimination in the presence of flanking distractors (Snow et al., 2009).

One interpretation of this hypothesis is that unilateral dorsal pulvinar inactivation should disrupt the mechanism to monitor and filter out distractors in the contralesional hemifield. If so, we should observe an increased selection of contralesional distractors. We found no inactivation-induced increase in false alarm rate when an easy or a difficult distractor was presented in the contralesional hemifield. An additional counterargument for the contralateral distractor filtering hypothesis can be derived from cued spatial attention tasks. The inactivation of the lateral pulvinar decreased the error rate due to contralesional distractors – i.e. decreased contralesional false alarm rate (Desimone et al., 1990), and similarly, the dorsal pulvinar inactivation caused increased reaction times when the (distracting invalid) cue was contralesional and the target ipsilesional (Petersen et al., 1987). Together, these findings question the dorsal pulvinar role in filtering out *contralesional* distractors. Instead, the pulvinar might be crucial for the contralateral spatial orienting and selective attention, as was also suggested in a number of patient studies (Danziger et al., 2001, 2004; Ward and Danziger, 2005; Ward and Arend, 2007).

In conclusion, this study demonstrates that dorsal pulvinar is involved in contralateral spatial orienting and resolving spatial competition, rather than in perceptual discrimination, even during the perceptual decision task. Future work should further investigate the neuronal basis of these effects in the pulvinar and in the connected cortical areas, and compare the role of the pulvinar to other subcortical structures such as the superior colliculus, known to mediate target selection and selective attention via thalamo-cortical pathways (Lovejoy and Krauzlis, 2017; Bogadhi et al., 2019; Klink et al., 2021).

## Authors contributions

KK, MW, and IK designed the experiments, KK collected the data and performed analyses, KK, MW, and IK wrote the paper.

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## Conflict of interest

The authors declare no competing financial interests.

## Data availability statement

The datasets generated and analyzed for the current study are available from the corresponding author on reasonable request.

# References


Adam R, Johnston K, Menon RS, Everling S (2020) Functional reorganization during the recovery of contralesional target selection deficits after prefrontal cortex lesions in macaque monkeys. NeuroImage 207:116339.

Arcaro MJ, Pinsk MA, Chen J, Kastner S (2018) Organizing principles of pulvino-cortical functional coupling in humans. Nature Communications 9:5382.

Arcaro MJ, Pinsk MA, Kastner S (2015) The Anatomical and Functional Organization of the Human Visual Pulvinar. Journal of Neuroscience 35:9848–9871.

Arend I, Machado L, Ward R, McGrath M, Ro T, Rafal RD (2008a) The role of the human pulvinar in visual attention and action: evidence from temporal-order judgment, saccade decision, and antisaccade tasks. Prog Brain Res 171:475–483.

Arend I, Rafal R, Ward R (2008b) Spatial and temporal deficits are regionally dissociable in patients with pulvinar lesions. Brain 131:2140–2152.

Baldwin MKL, Bourne JA (2017) The Evolution of Subcortical Pathways to the Extrastriate Cortex. In: Evolution of Nervous Systems, pp 165–185. Elsevier. Available at: http://linkinghub.elsevier.com/retrieve/pii/B9780128040423000816 [Accessed March 7, 2018].

Beck DM, Kastner S (2009) Top-down and bottom-up mechanisms in biasing competition in the human brain. Vision Research 49:1154–1165.

Bender DB, Butter CM (1987) Comparison of the effects of superior colliculus and pulvinar lesions on visual search and tachistoscopic pattern discrimination in monkeys. Exp Brain Res 69:140–154.

Bender DB, Youakim M (2001) Effect of Attentive Fixation in Macaque Thalamus and Cortex. Journal of Neurophysiology 85:219–234.

Benevento LA, Port JD (1995) Single neurons with both form/color differential responses and saccade-related responses in the nonretinotopic pulvinar of the behaving macaque monkey. Vis Neurosci 12:523–544.

Blatt GJ, Andersen RA, Stoner GR (1990) Visual receptive field organization and cortico-cortical connections of the lateral intraparietal area (area LIP) in the macaque. J Comp Neurol 299:421–445.

Bogadhi AR, Bollimunta A, Leopold DA, Krauzlis RJ (2019) Spatial Attention Deficits Are Causally Linked to an Area in Macaque Temporal Cortex. Current Biology 29:726-736.e4.

Bourgeois A, Guedj C, Carrera E, Vuilleumier P (2020) Pulvino-cortical interaction: An integrative role in the control of attention. Neuroscience & Biobehavioral Reviews 111:104–113.

Brainard DH (1997) The Psychophysics Toolbox. Spatial Vision 10:433–436.

Carrasco M (2011) Visual attention: The past 25 years. Vision Research 51:1484–1525.

Cisek P (2006) Integrated Neural Processes for Defining Potential Actions and Deciding between Them: A Computational Model. Journal of Neuroscience 26:9761–9770.

Corbetta M, Shulman GL (2011) Spatial neglect and attention networks. Annu Rev Neurosci 34:569–599.

Danziger S, Ward R, Owen V, Rafal R (2001) The effects of unilateral pulvinar damage in humans on reflexive orienting and filtering of irrelevant information. Behav Neurol 13:95–104.

Danziger S, Ward R, Owen V, Rafal R (2004) Contributions of the human pulvinar to linking vision and action. Cognitive, Affective, & Behavioral Neuroscience 4:89–99.

Desimone R, Wessinger M, Thomas L, Schneider W (1990) Attentional Control of Visual Perception: Cortical and Subcortical Mechanisms. Cold Spring Harbor Symposia on Quantitative Biology 55:963–971.

Dominguez-Vargas A-U, Schneider L, Wilke M, Kagan I (2017) Electrical Microstimulation of the Pulvinar Biases Saccade Choices and Reaction Times in a Time-Dependent Manner. J Neurosci 37:2234–2257.

Fetsch CR, Kiani R, Newsome WT, Shadlen MN (2014) Effects of Cortical Microstimulation on Confidence in a Perceptual Decision. Neuron 83:797–804.

Fiebelkorn IC, Pinsk MA, Kastner S (2018) A Dynamic Interplay within the Frontoparietal Network Underlies Rhythmic Spatial Attention. Neuron 99:842-853.e8.

Fiebelkorn IC, Pinsk MA, Kastner S (2019) The mediodorsal pulvinar coordinates the macaque fronto-parietal network during rhythmic spatial attention. Nature Communications 10:215.

Fischer J, Whitney D (2012) Attention gates visual coding in the human pulvinar. Nature Communications 3:1051.

Grieve KL, Acuña C, Cudeiro J (2000) The primate pulvinar nuclei: vision and action. Trends in neurosciences 23:35–39.

Gutierrez C, Cola MG, Seltzer B, Cusick C (2000) Neurochemical and connectional organization of the dorsal pulvinar complex in monkeys. Journal of Comparative Neurology 419:61–86.

Hardy SGP, Lynch JC (1992) The Spatial Distribution of Pulvinar Neurons That Project to Two Subregions of the Inferior Parietal Lobule in the Macaque. Cereb Cortex 2:217–230.

Kaas JH, Baldwin MKL (2020) The Evolution of the Pulvinar Complex in Primates and Its Role in the Dorsal and Ventral Streams of Cortical Processing. Vision 4:3.

Kaas JH, Lyon DC (2007) Pulvinar contributions to the dorsal and ventral streams of visual processing in primates. Brain Research Reviews 55:285–296.

Kagan I, Gibson L, Spanou E, Wilke M (2021) Effective connectivity and spatial selectivity-dependent fMRI changes elicited by microstimulation of pulvinar and LIP. NeuroImage 240:118283.

Karnath HO, Himmelbach M, Rorden C (2002) The subcortical anatomy of human spatial neglect: putamen, caudate nucleus and pulvinar. Brain 125:350–360.

Kastner S, O'Connor DH, Fukui MM, Fehd HM, Herwig U, Pinsk MA (2004) Functional imaging of the human lateral geniculate nucleus and pulvinar. J Neurophysiol 91:438–448.

Klink PC et al. (2021) Combining brain perturbation and neuroimaging in non-human primates. NeuroImage 235:118017.

Komura Y, Nikkuni A, Hirashima N, Uetake T, Miyamoto A (2013) Responses of pulvinar neurons reflect a subject's confidence in visual categorization. Nature Neuroscience 16:749–755.

LaBerge D, Buchsbaum MS (1990) Positron Emission Tomographic Measurements of Pulvinar Activity During an Attention Task. J Neurosci 10:613–619.

Li CS, Mazzoni P, Andersen RA (1999) Effect of reversible inactivation of macaque lateral intraparietal area on visual and memory saccades. J Neurophysiol 81:1827–1838.

Lovejoy LP, Krauzlis RJ (2010) Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. Nat Neurosci 13:261–266.

Lovejoy LP, Krauzlis RJ (2017) Changes in perceptual sensitivity related to spatial cues depends on subcortical activity. Proc Natl Acad Sci USA 114:6122–6126.

Lucas N, Bourgeois A, Carrera E, Landis T, Vuilleumier P (2019) Impaired visual search with paradoxically increased facilitation by emotional features after unilateral pulvinar damage. Cortex 120:223–239.

Luo TZ, Maunsell JHR (2015) Neuronal Modulations in Visual Cortex Are Associated with Only One of Multiple Components of Attention. Neuron 86:1182–1188.

Markowitz DA, Shewcraft RA, Wong YT, Pesaran B (2011) Competition for Visual Selection in the Oculomotor System. Journal of Neuroscience 31:9298–9306.

Ohayon S, Tsao DY (2012) MR-guided stereotactic navigation. J Neurosci Methods 204:389–397.

Petersen SE, Robinson DL, Morris JD (1987) Contributions of the pulvinar to visual spatial attention. Neuropsychologia 25:97–105.

Posner MI, Snyder CR, Davidson BJ (1980) Attention and the detection of signals. J Exp Psychol 109:160–174.

Preuss TM (2007) Evolutionary specializations of primate brain systems. In: Primate Origins: Evolution and Adaptations. (Ravosa MJ, Dagosto M, eds), pp 625-675. New York: Springer.

Prins N, Kingdom FAA (2009) Palamedes: Matlab routines for analyzing psychophysical data. Available at: http://www.palamedestoolbox.org.

Reynolds JH, Chelazzi L (2004) ATTENTIONAL MODULATION OF VISUAL PROCESSING. Annu Rev Neurosci 27:611–647.

Robinson DL, Petersen SE (1992) The pulvinar and visual salience. Trends in Neurosciences 15:127–132.

Robinson DL, Petersen SE, Keys W (1986) Saccade-related and visual activities in the pulvinar nuclei of the behaving rhesus monkey. Exp Brain Res 62 Available at: http://link.springer.com/10.1007/BF00236042 [Accessed January 4, 2021].

Romanski LM, Giguere M, Bates JF, Goldman-Rakic PS (1997) Topographic organization of medial pulvinar connections with the prefrontal cortex in the rhesus monkey. The Journal of comparative neurology 379:313–332.

Saalmann YB, Kastner S (2015) The cognitive thalamus. Front Syst Neurosci 9 Available at: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC4362213/ [Accessed October 27, 2015].

Schneider L, Dominguez-Vargas A-U, Gibson L, Kagan I, Wilke M (2019) Eye position signals in the dorsal pulvinar during fixation and goal-directed saccades. Journal of Neurophysiology 123:367–391.

Schneider L, Dominguez-Vargas A-U, Gibson L, Wilke M, Kagan I (2021) Visual, delay and oculomotor timing and tuning in macaque dorsal pulvinar during instructed and free choice memory saccades. bioRxiv 2021.12.21.473504 Available at: https://www.biorxiv.org/content/10.1101/2021.12.21.473504v1 [Accessed December 29, 2021].

Sherman SM, Guillery RW (2002) The role of the thalamus in the flow of information to the cortex. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1695–1708.

Shipp S (2003) The functional logic of cortico-pulvinar connections. Philosophical Transactions of the Royal Society B: Biological Sciences 358:1605–1624.

Snow JC, Allen HA, Rafal RD, Humphreys GW (2009) Impaired attentional selection following lesions to human pulvinar: evidence for homology between human and monkey. Proceedings of the National Academy of Sciences of the United States of America 106:4054–4059.

Stepniewska I (2003) The pulvinar complex. In: The Primate Visual System. CRC Press.

Strumpf H, Mangun GR, Boehler CN, Stoppel C, Schoenfeld MA, Heinze H-J, Hopf J-M (2013) The role of the pulvinar in distractor processing and visual search. Human Brain Mapping 34:1115–1132.

Ungerleider LG, Christensen CA (1977) Pulvinar lesions in monkeys produce abnormal eye movements during visual discrimination training. Brain Research 136:189–196.

Van der Stigchel S, Arend I, van Koningsbruggen MG, Rafal RD (2010) Oculomotor integration in patients with a pulvinar lesion. Neuropsychologia 48:3497–3504.

Ward R, Arend I (2007) An object-based frame of reference within the human pulvinar. Brain 130:2462–2469.

Ward R, Danziger S (2005) Selective attention and response control following damage to the human pulvinar. In: Attention in Action: Advances from Cognitive Neuroscience (Humphreys G, Riddoch J, eds), pp 325–350. New York: Psychology Press.

Wardak C, Ibos G, Duhamel JR, Olivier E (2006) Contribution of the monkey frontal eye field to covert visual attention. J Neurosci 26:4228–4235.

Wardak C, Olivier E, Duhamel JR (2002) Saccadic target selection deficits after lateral intraparietal area inactivation in monkeys. J Neurosci 22:9877–9884.

Wardak C, Olivier E, Duhamel JR (2004) A deficit in covert attention after parietal cortex inactivation in the monkey. Neuron 42:501–508.

Wilke M, Kagan I, Andersen RA (2012) Functional imaging reveals rapid reorganization of cortical activity after parietal inactivation in monkeys. PNAS 109:8274–8279.

Wilke M, Kagan I, Andersen RA (2013) Effects of Pulvinar Inactivation on Spatial Decision-making between Equal and Asymmetric Reward Options. Journal of Cognitive Neuroscience 25:1270–1283.

Wilke M, Mueller KM, Leopold DA (2009) Neural activity in the visual thalamus reflects perceptual suppression. Proc Natl Acad Sci U S A 106:9465–9470.

Wilke M, Turchi J, Smith K, Mishkin M, Leopold DA (2010) Pulvinar Inactivation Disrupts Selection of Movement Plans. Journal of Neuroscience 30:8650–8659.

Zhou H, Schafer RJ, Desimone R (2016) Pulvinar-Cortex Interactions in Vision and Attention. Neuron 89:209–220.

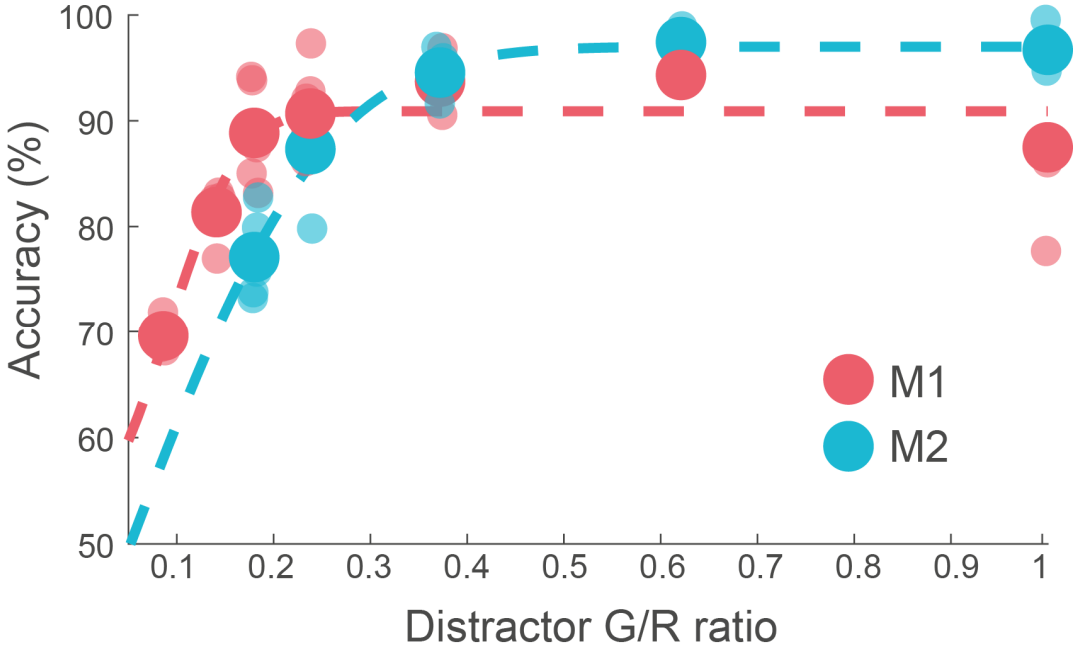
# Supplementary Information

**Dorsal pulvinar inactivation leads to spatial selection bias without perceptual deficit**

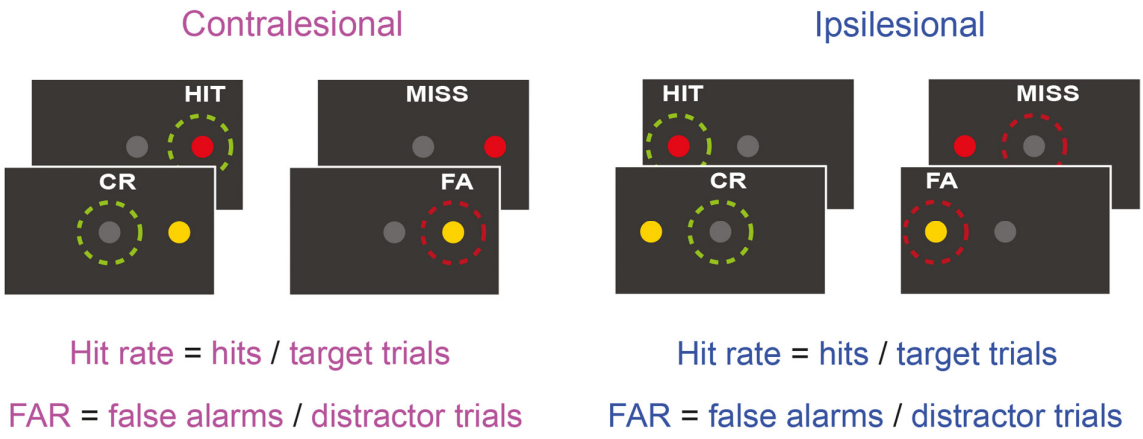
Kristin Kaduk, Melanie Wilke, Igor Kagan

6 Supplementary Figures

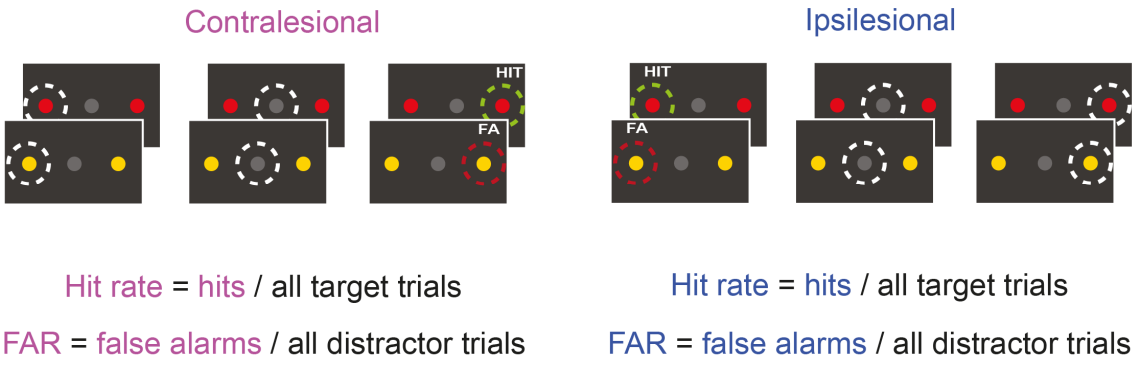
7 Supplementary Tables



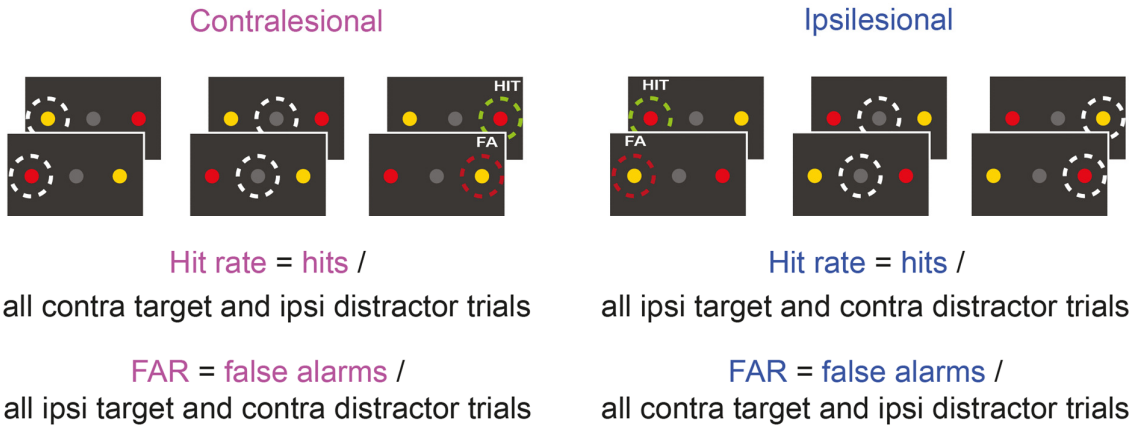

**Supplementary Figure S1.** Accuracy per distractor color. The monkeys performed a color discrimination paradigm with five distractor colors of different perceptual difficulty ranging from yellow (easy, G/R ratio: 1, RGB [60 60 0]) to red-orange (difficult, G/R ratio M1:0.08, M2:0.18, [M1: 128 11 0; M2: 128 23 0]). We calculated how accurate the target was discriminated from a distractor in the opposite hemifield. The large dots display the mean accuracy across sessions for the different applied G/R ratios separated for each monkey. To these accuracy values, the cumulative normal function was fitted. The small transparent dots display the accuracy per session. The goal of the assessment was to determine a distractor color that could be correctly discriminated from the target with 70 - 80% accuracy, for the difficult perceptual condition (G/R ratio M1:0.08, M2:0.18).



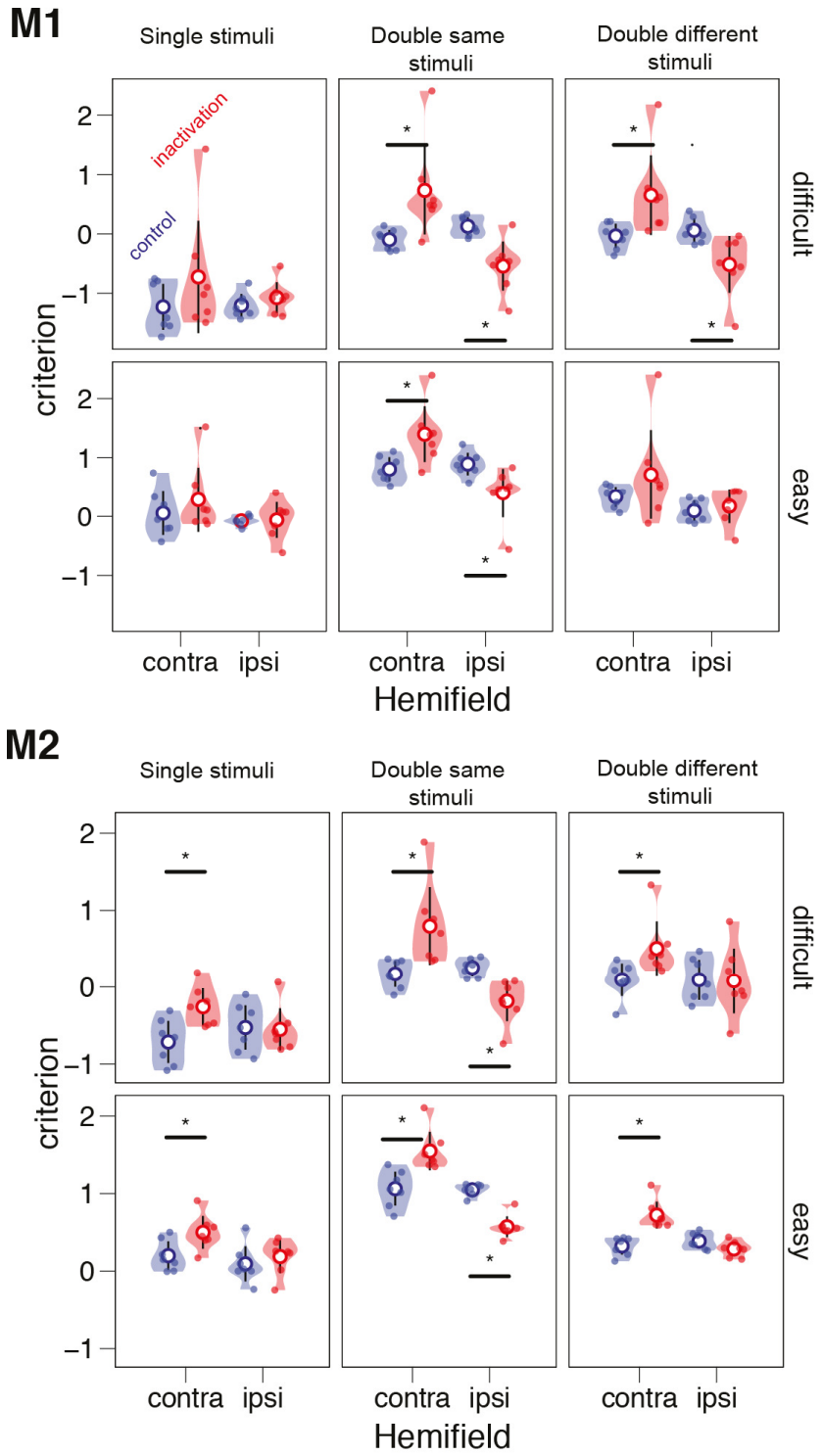

**Supplementary Figure S2.** Calculation of the signal detection theory variables for single stimuli related to the results in Figure 4. Here we describe, firstly, how trials were classified in relation to the monkey's responses and secondly, the calculations. Hits are trials where a saccade was made to a target (correct response, green dashed circle). Misses are trials where the monkey fixated the dot in the middle of the screen while a single target was displayed (incorrect response, dark red dashed circle). Correct rejections are trials where the monkey fixated the dot in the middle of the screen when a single distractor was displayed in the periphery (correct response, green dashed circle). False alarms are trials where the monkey made a saccade to the distractor (incorrect response, dark red dashed circle). We calculated the hit rate and false alarm rate (FAR) according to Hit rate = Hits / contralesional target trials and False alarm rate = False alarms / contralesional distractor trials. We used the standard calculations for the dprime (d' = z (Hit) –z(FAR)) and criterion (c = -0.5*(z(Hit) + z(FAR))). All variables were calculated separately for stimuli presented in the ipsilesional and contralesional hemifield to compare the changes in dprime and criterion for each hemifield.



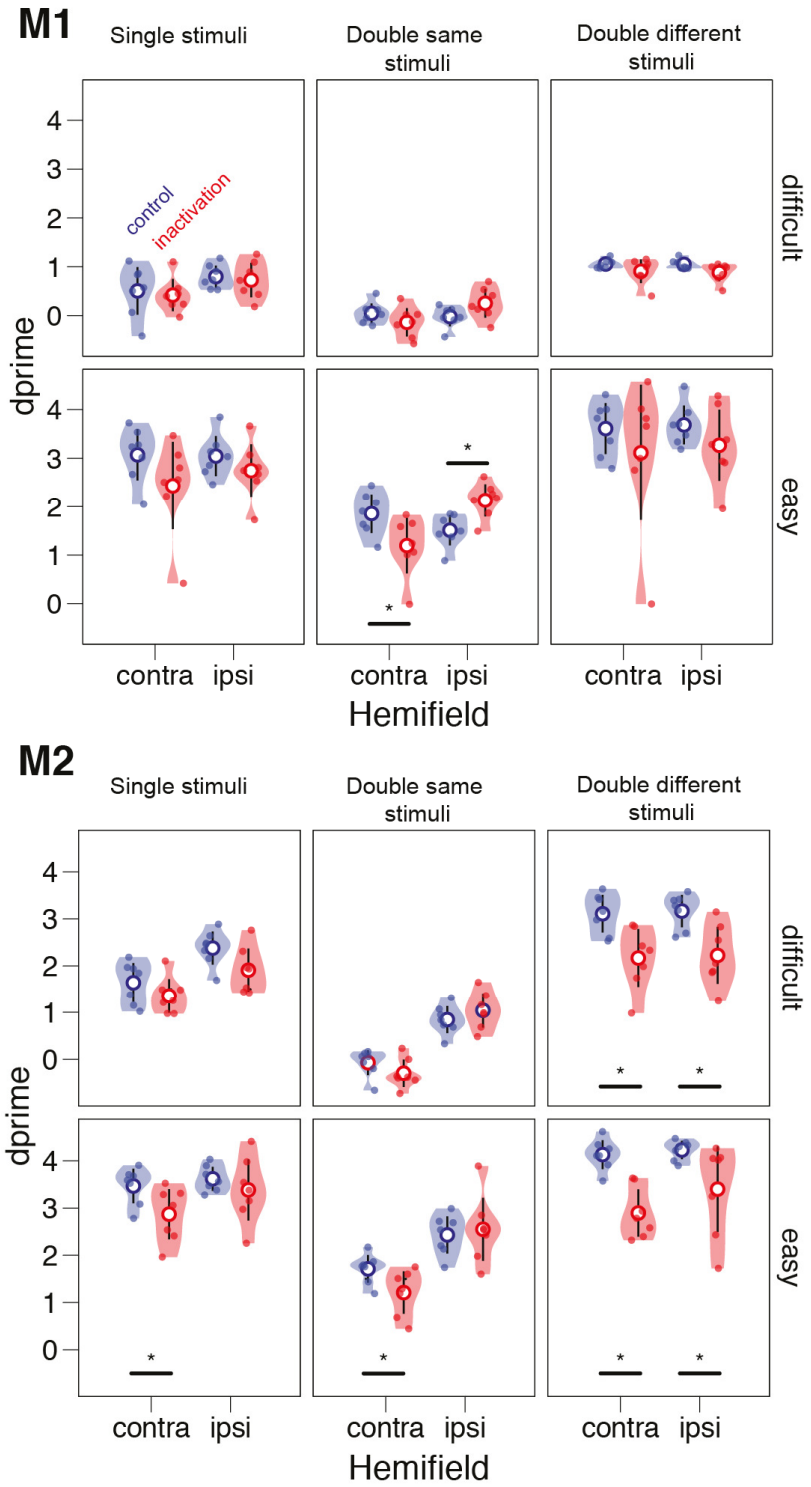

**Supplementary Figure S3.** Calculation of the signal detection theory variables for double same stimuli related to the results in Figure 5. Notations are the same as in **Suppl. Figure 2**. All variables were calculated separately for stimuli presented in the ipsilesional or contralesional hemifield, which allows us to compare the changes in dprime and criterion for each hemifield. In the following, the examples are given for the contralesional hemifield. Contralesional hits are trials where a saccade was made to the contralesional target when a target was presented in each hemifield. Contralesional false alarms are trials where a saccade was made to the contralesional distractor when a distractor was presented in each hemifield. Hit rate is computed as all contralesional hits divided by all double same target trials. False alarm rate is computed as all contralesional false alarms divided by all double same distractor trials. We used the standard calculations for the dprime (d' = z(Hit) –z(FAR)) and criterion (c = -0.5*(z(Hit) + z(FAR))).




**Supplementary Figure S4.** Calculation of the signal detection theory variables for double different stimuli related to the results in Figure 6. Notations are the same as in **Suppl. Figure 2**. All variables were calculated separately for stimuli presented in the ipsilesional or contralesional hemifield, which allows us to compare the changes in dprime and criterion for each hemifield. In the following, examples are given for the ipsilesional hemifield. Ipsilesional hits are trials where a saccade was made to the ipsilesional target. Ipsilesional false alarms are trials where a saccade was made to the ipsilesional distractor. The hit rate is computed as all ipsilesional hits divided by all double different trials where a target was presented in the ipsilesional hemifield (including all response options, i.e. fixation and saccades to either ipsi- or contralesional stimulus). Likewise, false alarm rate (FAR) is computed as all ipsilesional false alarms divided by all double different trials where a distractor was presented in the ipsilesional hemifield. We used the standard calculations for the dprime (d' = z(Hit) –z(FAR)) and criterion (c = -0.5*(z(Hit) + z(FAR)).




**Supplementary Figure S5.** Summary of the results for the criterion. The violin plots display the distribution of the computed values for the criterion for the two difficulty levels (difficult and easy), stimulus types (single / double same / double different Stimuli), and hemifield (contra-/ipsi-lesional) for control (blue) and inactivation (red) sessions. The mean is displayed with an empty circle and 95% confidence intervals. Each small colored dot represents a session. The stars display the significance of the t-test at the p-value < 0.05.




**Supplementary Figure S6.** Summary of the results for the dprime. The violin plots display the distribution of the computed values for the criterion for the two difficulty levels (difficult and easy), stimulus types (single / double same / double different Stimuli), and hemifield (contra-/ipsi-lesional) for control (blue) and inactivation (red) sessions. The mean is displayed with an empty circle and 95% confidence intervals. Each small colored dot represents a session. The stars display the significance of the t-test at the p-value < 0.05.

**Supplementary Table S1.** Three-way mixed ANOVA on saccade latency, with within-factors “Stimulus Type” (Single / Double same / Double different) and “Hemifield” (contralesional/ipsilesional) and between-factor “Perturbation” (control/inactivation sessions); ges - generalized eta squared. Significant effects are shown in bold font.

| Factor | DFn | DFd | F | p | p<.05 | ges | Monkey |
|---|---|---|---|---|---|---|---|
| **Perturbation** | **1** | **11** | **5.96** | **0.033** | * | **0.24** | M1 |
| **Hemifield** | **1** | **11** | **20.08** | **0.001** | * | **0.18** | |
| **Stimulus Type** | **2** | **22** | **25.29** | **< .001** | * | **0.20** | |
| **Perturbation:Hemifield** | **1** | **11** | **21.81** | **0.001** | * | **0.20** | |
| **Perturbation:Stimulus Type** | **2** | **22** | **5.25** | **0.014** | * | **0.05** | |
| Hemifield:Stimulus Type | 2 | 22 | 1.12 | 0.344 | | 0.02 | |
| **Perturbation:Hemifield:Stimulus Type** | **2** | **22** | **4.64** | **0.021** | * | **0.07** | |
| | | | | | | | |
| **Perturbation** | **1** | **12** | **7.48** | **0.018** | * | **0.26** | M2 |
| **Hemifield** | **1** | **12** | **6.72** | **0.024** | * | **0.15** | |
| **Stimulus Type** | **2** | **24** | **14.19** | **< .001** | * | **0.08** | |
| Perturbation:Hemifield | 1 | 12 | 3.47 | 0.087 | | 0.08 | |
| Perturbation:Stimulus Type | 2 | 24 | 1.27 | 0.299 | | 0.01 | |
| **Hemifield:Stimulus Type** | **2** | **24** | **11.44** | **< .001** | * | **0.05** | |
| **Perturbation:Hemifield:Stimulus Type** | **2** | **24** | **3.74** | **0.039** | * | **0.02** | |

**Supplementary Table S2.** Multiple comparison tests of the different stimulus types for the control sessions on the accuracy, separately for each perceptual difficulty (Difficult/Easy discrimination). Significant effects are shown in bold font.

| Comparison (Control Sessions) | Difficulty | 95% Confidence Intervals | p | p<.05 | Monkey |
|---|---|---|---|---|---|
| Single Stimuli vs. Double Same Stimuli | difficult | **7.85, 21.97** | **< .001** | * | M1 |
| Single Stimuli vs. Double Different Stimuli | difficult | **-20.54, - 6.41** | **< .001** | * | |
| Double Same Stimuli vs. Double Different | difficult | **-35.45, -21.30** | **< .001** | * | |
| Single Stimuli vs. Double Same Stimuli | easy | -3.66, 0.93 | .4 | | |
| Single Stimuli vs. Double Different Stimuli | easy | -2.63, 1.94 | .9 | | |
| Double Same Stimuli vs. Double Different | easy | -1.28, 3.31 | .7 | | |
| Single Stimuli vs. Double Same Stimuli | difficult | **1.92, 8.17** | **.001** | * | M2 |
| Single Stimuli vs. Double Different Stimuli | difficult | **-16.91, -10.65** | **< .001** | * | |
| Double Same Stimuli vs. Double Different | difficult | **-21.96, 15.71** | **< .001** | * | |
| Single Stimuli vs. Double Same Stimuli | easy | -5.96, 2.35 | .8 | | |
| Single Stimuli vs. Double Different Stimuli | easy | -5.36, 2.96 | .9 | | |
| Double Same Stimuli vs. Double Different | easy | -3.56, 4.77 | .9 | | |

**Supplementary Table S3.** Three-way mixed ANOVA on accuracy, with within-factors “Stimulus Type” (Single / Double Same / Double different) and “Difficulty” (Difficult/Easy discrimination) and between-factor “Perturbation” (control/inactivation sessions); ges - generalized eta squared. Significant effects are shown in bold font.

| Factor | DFn | DFd | F | p | p<.05 | ges | Monkey |
|---|---|---|---|---|---|---|---|
| Perturbation | 1 | 12 | 1.46 | 0.250 | | 0.06 | |
| **Difficulty** | **1** | **12** | **349.71** | **< .001** | ***** | **0.87** | |
| **Stimulus Type** | **2** | **24** | **6.09** | **.007** | ***** | **0.11** | |
| Perturbation:Difficulty | 1 | 12 | 1.36 | .275 | | 0.03 | M1 |
| Perturbation:Stimulus Type | 2 | 24 | 3.17 | .060 | | 0.06 | |
| **Difficulty:Stimulus Type** | **2** | **24** | **124.01** | **< .001** | ***** | **0.29** | |
| Perturbation:Difficulty:Stimulus Type | 2 | 24 | 1.88 | .175 | | 0.01 | |
| | | | | | | | |
| **Perturbation** | **1** | **12** | **9.42** | **.010** | ***** | **0.22** | |
| **Difficulty** | **1** | **12** | **421.89** | **< .001** | ***** | **0.72** | |
| **Stimulus Type** | **2** | **24** | **8.12** | **.002** | ***** | **0.24** | |
| Perturbation:Difficulty | 1 | 12 | 0.07 | .798 | | 0.0004 | M2 |
| **Perturbation:Stimulus Type** | **2** | **24** | **6.40** | **.006** | ***** | **0.20** | |
| **Difficulty:Stimulus Type** | **2** | **24** | **104.36** | **< .001** | ***** | **0.48** | |
| Perturbation:Difficulty:Stimulus Type | 2 | 24 | 1.12 | .342 | | 0.01 | |

**Supplementary Table S4.** Four-way mixed ANOVA on dprime and criterion with within-factor “Stimuls type” (single / double same / double different), “Difficulty” (easy / difficult), and “Hemifield” (contralesional / ipsilesional) and between-factor “Perturbation” (control / inactivation sessions), separately for each stimulus type, for the difficult discrimination; ges - generalized eta squared. Significant effects are shown in bold font.

| Factor | DFn | DFd | F | p | p<.05 | ges | DV | Monkey |
|---|---|---|---|---|---|---|---|---|
| Perturbation | 1 | 12 | 2.69 | .127 | | 0.03 | criterion | M1 |
| Hemifield | 1 | 12 | 3.42 | .089 | | 0.17 | | |
| **Difficulty** | **1** | **12** | **611.4** | **< .001** | ***** | **0.43** | | |
| **Stimulus Type** | **2** | **24** | **220.5** | **< .001** | ***** | **0.48** | | |
| Perturbation:Hemifield | 1 | 12 | 3.6 | .081 | | 0.18 | | |
| Perturbation:Difficulty | 1 | 12 | 0.09 | .767 | | < 0.01 | | |
| Perturbation:Stimulus Type | 2 | 24 | 1.35 | .279 | | 0.01 | | |
| Hemifield:Difficulty | 1 | 12 | 0.56 | .467 | | < 0.01 | | |
| **Hemifield:Stimulus Type** | **2** | **24** | **7.14** | **.004** | ***** | **0.02** | | |
| **Difficulty:Stimulus Type** | **2** | **24** | **47.64** | **< .001** | ***** | **0.14** | | |
| **Perturbation:Hemifield:Difficulty** | **1** | **12** | **17.86** | **.001** | ***** | **0.02** | | |
| **Perturbation:Hemifield:Stimulus Type** | **2** | **24** | **17.30** | **< .001** | ***** | **0.05** | | |
| Perturbation:Difficulty:Stimulus Type | 2 | 24 | 2.36 | .116 | | 0.01 | | |
| Hemifield:Difficulty:Stimulus Type | 2 | 24 | 2.71 | .087 | | < 0.01 | | |
| **Perturbation:Hemifield:Difficulty:Stimulus Type** | **2** | **24** | **8.69** | **.001** | ***** | **0.01** | | |
| Perturbation | 1 | 12 | 1.42 | .257 | | 0.03 | dprime | |
| Hemifield | 1 | 12 | 3.98 | .069 | | 0.03 | | |
| **Difficulty** | **1** | **12** | **227.7** | **< .001** | ***** | **0.81** | | |
| **Stimulus Type** | **2** | **24** | **105.2** | **< .001** | ***** | **0.55** | | |
| Perturbation:Hemifield | 1 | 12 | 4.61 | .053 | | 0.03 | | |
| Perturbation:Difficulty | 1 | 12 | 0.82 | .383 | | 0.02 | | |
| Perturbation:Stimulus Type | 2 | 24 | 1.75 | .196 | | 0.02 | | |
| Hemifield:Difficulty | 1 | 12 | 0.07 | .796 | | < 0.01 | | |
| Hemifield:Stimulus Type | 2 | 24 | 0.82 | .452 | | 0.01 | | |
| **Difficulty:Stimulus Type** | **2** | **24** | **19.85** | **< .001** | ***** | **0.10** | | |
| Perturbation:Hemifield:Difficulty | 1 | 12 | 2.26 | .159 | | 0.01 | | |
| **Perturbation:Hemifield:Stimulus Type** | **2** | **24** | **3.99** | **.032** | ***** | **0.03** | | |
| Perturbation:Difficulty:Stimulus Type | 2 | 24 | 0.81 | .459 | | 0.01 | | |
| Hemifield:Difficulty:Stimulus Type | 2 | 24 | 3.13 | .062 | | 0.01 | | |
| **Perturbation:Hemifield:Difficulty:Stimulus Type** | **2** | **24** | **3.87** | **.035** | ***** | **0.01** | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Perturbation** | **1** | **12** | **6.71** | **.024** | * | **0.23** | criterion | M1 |
| **Hemifield** | **1** | **12** | **9.48** | **.01** | * | **0.60** | | |
| **Difficulty** | **1** | **12** | **542.2** | **< .001** | * | **0.64** | | |
| **Stimulus Type** | **2** | **24** | **202.1** | **< .001** | * | **0.28** | | |
| **Perturbation:Hemifield** | **1** | **12** | **12.14** | **< .001** | * | **0.01** | | |
| Perturbation:Difficulty | 1 | 12 | 1.03 | .330 | | 0.02 | | |
| Perturbation:Stimulus Type | 2 | 24 | 2.22 | .130 | | 0.01 | | |
| Hemifield:Difficulty | 1 | 12 | 0.56 | .469 | | 0.08 | | |
| **Hemifield:Stimulus Type** | **2** | **24** | **7.99** | **.002** | * | **0.22** | | |
| **Difficulty:Stimulus Type** | **2** | **24** | **104.9** | **< .001** | * | **0.01** | | |
| Perturbation:Hemifield:Difficulty | 1 | 12 | 0.39 | .547 | | 0.08 | | |
| **Perturbation:Hemifield:Stimulus Type** | **2** | **24** | **7.82** | **.002** | * | **0.01** | | |
| Perturbation:Difficulty:Stimulus Type | 2 | 24 | 0.33 | .723 | | 0.01 | | |
| Hemifield:Difficulty:Stimulus Type | 2 | 24 | 0.82 | .454 | | 0.01 | | |
| Perturbation:Hemifield:Difficulty:Stimulus Type | 2 | 24 | 0.74 | .486 | | 0.23 | | |
| **Perturbation** | **1** | **12** | **10.0** | **.008** | * | **0.29** | dprime | |
| **Hemifield** | **1** | **12** | **41.4** | **< .001** | * | **0.69** | | |
| **Difficulty** | **1** | **12** | **591.4** | **< .001** | * | **0.77** | | |
| **Stimulus Type** | **2** | **24** | **179.9** | **< .001** | * | **0.02** | | |
| Perturbation:Hemifield | 1 | 12 | 2.24 | .160 | | 0.01 | | |
| Perturbation:Difficulty | 1 | 12 | 0.82 | .382 | | 0.14 | | |
| **Perturbation:Stimulus Type** | **2** | **24** | **8.76** | **.001** | * | **0.01** | | |
| Hemifield:Difficulty | 1 | 12 | 0.19 | .674 | | 0.14 | | |
| **Hemifield:Stimulus Type** | **2** | **24** | **18.44** | **< .001** | * | **0.08** | | |
| **Difficulty:Stimulus Type** | **2** | **24** | **21.91** | **< .001** | * | **0.01** | | |
| Perturbation:Hemifield:Difficulty | 1 | 12 | 2.33 | .153 | | 0.01 | | |
| Perturbation:Hemifield:Stimulus Type | 2 | 24 | 1.11 | .346 | | 0.01 | | |
| Perturbation:Difficulty:Stimulus Type | 2 | 24 | 0.26 | .774 | | 0.01 | | |
| **Hemifield:Difficulty:Stimulus Type** | **2** | **24** | **3.48** | **.047** | * | **0.02** | | |
| Perturbation:Hemifield:Difficulty:Stimulus Type | 2 | 24 | 0.33 | .721 | | < 0.01 | | |

**Supplementary Table S5.** Two-way mixed ANOVA on dprime and criterion with within-factor "Hemifield" (contralesional/ipsilesional) and between-factor "Perturbation" (control/inactivation sessions), separately for each stimulus type, **for the difficult discrimination**; ges - generalized eta squared. Significant effects are shown in bold font.

| Factor | DFn | DFd | F | p | p<.05 | ges | DV | Monkey | Stimulus type |
|---|---|---|---|---|---|---|---|---|---|
| Perturbation | 1 | 12 | 2.23 | .161 | | 0.08 | criterion | M1 | Single |
| Hemifield | 1 | 12 | 0.51 | .489 | | 0.02 | | | |
| Perturbation:Hemifield | 1 | 12 | 0.70 | .420 | | 0.03 | | | |
| Perturbation | 1 | 12 | 0.31 | .588 | | 0.01 | dprime | | |
| Hemifield | 1 | 12 | 3.77 | .076 | | 0.15 | | | |
| Perturbation:Hemifield | 1 | 12 | 0.003 | .960 | | < 0.01 | | | |
| Perturbation | 1 | 12 | 3.09 | .104 | | 0.14 | criterion | M2 | |
| Hemifield | 1 | 12 | 0.31 | .590 | | < 0.01 | | | |
| **Perturbation:Hemifield** | **1** | **12** | **6.40** | **.026** | * | **0.17** | | | |
| Perturbation | 1 | 12 | 3.46 | .087 | | 0.18 | dprime | | |
| **Hemifield** | **1** | **12** | **33.58** | **< .001** | * | **0.39** | | | |
| Perturbation:Hemifield | 1 | 12 | 0.68 | .425 | | 0.01 | | | |
| | | | | | | | | | |
| Perturbation | 1 | 12 | 1.11 | .313 | | 0.01 | criterion | M1 | Double Same |
| Hemifield | 1 | 12 | 4.72 | .051 | | 0.26 | | | |
| **Perturbation:Hemifield** | **1** | **12** | **9.65** | **.009** | * | **0.42** | | | |
| Perturbation | 1 | 12 | 0.76 | .401 | | 0.01 | dprime | | |
| Hemifield | 1 | 12 | 1.42 | .256 | | 0.09 | | | |
| Perturbation:Hemifield | 1 | 12 | 2.89 | .115 | | 0.17 | | | |
| Perturbation | 1 | 12 | 2.62 | .132 | | 0.02 | criterion | M2 | |
| **Hemifield** | **1** | **12** | **7.43** | **.018** | * | **0.36** | | | |
| **Perturbation:Hemifield** | **1** | **12** | **10.45** | **.007** | * | **0.44** | | | |
| Perturbation | 1 | 12 | 0.02 | .888 | | 0.01 | dprime | | |
| **Hemifield** | **1** | **12** | **55.80** | **< .001** | * | **0.77** | | | |
| Perturbation:Hemifield | 1 | 12 | 1.95 | .188 | | 0.11 | | | |
| | | | | | | | | | |
| Perturbation | 1 | 12 | 1.86 | .198 | | 0.01 | criterion | M1 | Double Different |
| Hemifield | 1 | 12 | 4.67 | .052 | | 0.28 | | | |
| **Perturbation:Hemifield** | **1** | **12** | **6.47** | **.026** | * | **0.34** | | | |
| Perturbation | 1 | 12 | 2.91 | .114 | | 0.19 | dprime | | |
| Hemifield | 1 | 12 | 0.90 | .361 | | 0.01 | | | |
| Perturbation:Hemifield | 1 | 12 | 0.32 | .582 | | 0.01 | | | |
| **Perturbation** | **1** | **12** | **6.88** | **.022** | * | **0.09** | **criterion** | M2 | |
| Hemifield | 1 | 12 | 1.55 | .237 | | 0.1 | | | |
| Perturbation:Hemifield | 1 | 12 | 1.53 | .240 | | 0.1 | | | |
| **Perturbation** | **1** | **12** | **10.73** | **.007** | * | **0.46** | **dprime** | | |
| Hemifield | 1 | 12 | 1.23 | .289 | | < 0.01 | | | |
| Perturbation:Hemifield | 1 | 12 | < 0.01 | .993 | | < 0.01 | | | |

**Supplementary Table S6.** Two-way mixed ANOVA on dprime and criterion with within-factor "Hemifield" (contralesional/ipsilesional) and between-factor "Perturbation" (control/inactivation sessions), separately for each stimulus type, **for the easy discrimination**; ges - generalized eta squared. Significant effects are shown in bold font.

| Factor | DFn | DFd | F | p | p<.05 | ges | DV | Monkey | Stimulus type |
|---|---|---|---|---|---|---|---|---|---|
| Perturbation | 1 | 12 | 1.14 | .306 | | 0.027 | criterion | M1 | Single |
| Hemifield | 1 | 12 | 1.82 | .202 | | 0.097 | criterion | | |
| Perturbation:Hemifield | 1 | 12 | 0.37 | .557 | | 0.021 | criterion | | |
| Perturbation | 1 | 12 | 2.09 | .174 | | 0.124 | dprime | | |
| Hemifield | 1 | 12 | 0.84 | .378 | | 0.013 | dprime | | |
| Perturbation:Hemifield | 1 | 12 | 1.16 | .302 | | 0.018 | dprime | | |
| Perturbation | 1 | 12 | 4.59 | .053 | | 0.182 | criterion | M2 | |
| **Hemifield** | **1** | **12** | **7.13** | **.020** | ***** | **0.200** | **criterion** | | |
| Perturbation:Hemifield | 1 | 12 | 1.73 | .213 | | 0.057 | criterion | | |
| Perturbation | 1 | 12 | 3.50 | .086 | | 0.161 | dprime | | |
| Hemifield | 1 | 12 | 4.34 | .059 | | 0.110 | dprime | | |
| Perturbation:Hemifield | 1 | 12 | 1.28 | .279 | | 0.035 | dprime | | |
| | | | | | | | | | |
| Perturbation | 1 | 12 | 0.62 | .445 | | 0.005 | criterion | M1 | Double Same |
| **Hemifield** | **1** | **12** | **5.85** | **.032** | ***** | **0.306** | **criterion** | | |
| **Perturbation:Hemifield** | **1** | **12** | **8.30** | **.014** | ***** | **0.385** | **criterion** | | |
| Perturbation | 1 | 12 | 0.02 | .899 | | 0.001 | dprime | | |
| Hemifield | 1 | 12 | 2.56 | .135 | | 0.112 | dprime | | |
| **Perturbation:Hemifield** | **1** | **12** | **11.99** | **.005** | ***** | **0.370** | **dprime** | | |
| Perturbation | 1 | 12 | 0.004 | .949 | | 0.001 | criterion | M2 | |
| **Hemifield** | **1** | **12** | **33.18** | **< .001** | ***** | **0.651** | **criterion** | | |
| **Perturbation:Hemifield** | **1** | **12** | **31.20** | **< .001** | ***** | **0.637** | **criterion** | | |
| Perturbation | 1 | 12 | 2.052 | .178 | | 0.039 | dprime | | |
| **Hemifield** | **1** | **12** | **18.84** | **< .001** | ***** | **0.544** | **dprime** | | |
| Perturbation:Hemifield | 1 | 12 | 1.72 | .215 | | 0.098 | dprime | | |
| | | | | | | | | | |
| Perturbation | 1 | 12 | 3.93 | .071 | | 0.069 | criterion | M1 | Double Different |
| Hemifield | 1 | 12 | 3.29 | .095 | | 0.175 | criterion | | |
| Perturbation:Hemifield | 1 | 12 | 0.49 | .498 | | 0.031 | criterion | | |
| Perturbation | 1 | 12 | 0.98 | .342 | | 0.067 | dprime | | |
| Hemifield | 1 | 12 | 0.46 | .511 | | 0.004 | dprime | | |
| Perturbation:Hemifield | 1 | 12 | 0.05 | .823 | | 0.000 | dprime | | |
| **Perturbation** | **1** | **12** | **9.52** | **< .001** | ***** | **0.267** | **criterion** | M2 | |
| **Hemifield** | **1** | **12** | **12.78** | **.0040** | ***** | **0.365** | **criterion** | | |
| **Perturbation:Hemifield** | **1** | **12** | **22.96** | **< .001** | ***** | **0.508** | **criterion** | | |
| **Perturbation** | **1** | **12** | **13.50** | **< .001** | ***** | **0.469** | **dprime** | | |
| Hemifield | 1 | 12 | 4.24 | .062 | | 0.070 | dprime | | |
| Perturbation:Hemifield | 1 | 12 | 1.94 | .189 | | 0.033 | dprime | | |

**Supplementary Table S7.** Non-hemifield-specific bias ("stay" – central fixation option, vs. "go" – saccade to a peripheral stimulus) in control and inactivation sessions. The negative criterion indicated a "Go" bias. The table shows the results of the two-sided t-test against zero.

| Monkey | Difficulty | Session type | Stimulus type | Criterion | t-value | p-value | Bias |
|---|---|---|---|---|---|---|---|
| M1 | difficult | control | single stimuli | -1.21 | -11.16 | < .001 | Go |
| | | inactivation | | -0.89 | -4.73 | .003 | Go |
| | easy | control | | 0.01 | 0.13 | .903 | Neutral |
| | | inactivation | | 0.10 | 1.46 | .196 | Neutral |
| | difficult | control | double same stimuli | -2.25 | -27.63 | < .001 | Go |
| | | inactivation | | -2.17 | -14.83 | < .001 | Go |
| | easy | control | | -0.54 | -10.33 | < .001 | Go |
| | | inactivation | | -0.49 | -7.05 | < .001 | Go |
| | difficult | control | double different stimuli | 0.01 | 2.64 | .039 | Stay |
| | | inactivation | | 0.02 | 2.93 | .026 | Stay |
| | easy | control | | 0.23 | 8.4 | < .001 | Stay |
| | | inactivation | | 0.41 | 5.37 | .002 | Stay |
| M2 | difficult | control | single stimuli | -0.65 | -5.8 | .001 | Go |
| | | inactivation | | -0.38 | -6.5 | .001 | Go |
| | easy | control | | 0.15 | 2.25 | .065 | Neutral |
| | | inactivation | | 0.5 | 6.39 | .001 | Stay |
| | difficult | control | double same stimuli | -1.36 | -19.69 | < .001 | Go |
| | | inactivation | | -1.04 | -9.96 | < .001 | Go |
| | easy | control | | -0.18 | -2.14 | .076 | Neutral |
| | | inactivation | | 0.09 | 1.04 | .340 | Neutral |
| | difficult | control | double different stimuli | 0.08 | 2.79 | .032 | Stay |
| | | inactivation | | 0.27 | 3.91 | .008 | Stay |
| | easy | control | | 0.41 | 11.35 | < .001 | Stay |
| | | inactivation | | 0.61 | 9.5 | < .001 | Stay |