Effect of Viewing Distance On Object Responses In Macaque Areas 45B, F5a And F5p

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Effect of viewing distance on object responses in macaque areas 45B, F5a and F5p

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Abstract

To perform tasks like grasping, the brain has to process visual object information so that the grip aperture can be adjusted before touching the object. Previous studies have demonstrated that the posterior subsector of the Anterior Intraparietal area (pAIP) is connected to area 45B, and its anterior counterpart (aAIP) to F5a. However, the role of area 45B and F5a in visually-guided grasping is poorly understood. Here, we investigated the role of area 45B, F5a and F5p in object processing during visually-guided grasping in two monkeys. If the presentation of an object activates a motor command related to the preshaping of the hand, as in F5p, such neurons should prefer objects presented within reachable distance. Conversely, neurons encoding a purely visual representation of an object – possibly in area 45B and F5a – should be less affected by viewing distance. Contrary to our expectations, we found that most neurons in area 45B were object- and viewing distance-selective (mostly Near-preferring). Area F5a showed much weaker object selectivity compared to 45B, with a similar preference for objects presented at the Near position. Finally, F5p neurons were less object selective and frequently Far-preferring. In sum, area 45B – but not F5p– prefers objects presented in peripersonal space.

Introduction

Different brain areas in the dorsal visual stream and its target areas in frontal cortex contribute to object grasping. Although neurons in parietal area V6A also respond during object grasping [1-3], the most studied parieto-frontal network for controlling the hand comprises the Anterior Intraparietal Area (AIP), the ventral premotor cortex (PMv) and primary motor cortex (M1). AIP neurons are selective for real-world objects [4], grip type [5] (Baumann et al., 2009), 3D [6] and 2D images of objects and very small fragments [7,8]. Overall, the target areas of AIP in frontal cortex seem to have similar properties. Neurons in the anterior subsector of PMv (F5a), which is connected to 3D-shape selective sites in the anterior subsector of AIP (aAIP [9]), respond selectively to images of 3D objects [10] and during object grasping. Visual-dominant neurons (i.e., responding during object fixation but not during grasping in the dark) are present in F5a [10] but not in F5p [4,11]. A subset of neurons in the posterior part of PMv (F5p) are selective for real-world objects, even during passive fixation[11]. In area F5p, objects are represented mainly in terms of the grip type used to grasp the object[4]. Instead, area 45B, in the anterior bank of the lower ramus of the arcuate sulcus and receiving input from 3D-shape selective sites in the posterior subsector of AIP (pAIP [9]), responds selectively to 2D images of objects and to very small contour fragments, as in pAIP [12]. Other parts of AIP are also connected to the F5p subsector in PMv [13] .

Few studies have investigated the neural representation of space at the single-cell level in parietal [14,15] and frontal cortex [16,17]. Lesion studies in monkeys [18] and humans [19] have indicated the existence of distinct networks processing near and far space. [20] have shown that visual stimuli in near space activate temporal, parietal, prefrontal and premotor areas, whereas stimuli in far space produced activations in a different network spanning occipital, temporal, parietal, cingulate and orbitofrontal cortex, as suggested by human studies [21,22]. To date, no study has investigated the other two subsectors of area F5 (F5a, F5p) and area 45B concerning space processing.

We investigated the encoding of viewing distance in three frontal areas receiving input from AIP. Any neuronal response to the presentation of an object could reflect either the activation of the motor plan to grasp the object, or a visual representation of the object, which is later transformed into a motor plan. If a neuron’s response to objects mainly reflects the motor plan to grasp that object (as in F5p), this response should be strongly modulated by viewing distance, since objects appearing in extrapersonal space should not activate the motor plan to the same degree. If a neuron encodes object information in visual terms (as we expect in 45B and in a subset of neurons in F5a), the neuronal object responses in near and far space should be similar, provided that retinal size is constant. To maximize the activation of a motor plan, we randomly interleaved fixation trials and grasping trials when the object was presented in peripersonal space without informing the animals.

3. Materials and methods

3.1 Subjects and Surgery

Two adult male rhesus monkeys (D, 7 kg and Y, 12.5 kg) served as subjects for the experiments. All experimental procedures, surgical techniques, and veterinary care were performed in accordance with the NIH Guide for Care and Use of Laboratory Animals and in accordance with the European Directive 2010/63/EU and were approved by the local Ethical Committee Animal Experimentation (ECD) of the KU Leuven.

An MRI-compatible head fixation post and recording chamber were implanted during propofol anesthesia using dental acrylic and ceramic screws above the right arcuate sulcus in Monkey D and over the left arcuate sulcus in Monkey Y. The recording chamber allowed us to access 45B, F5a and F5p, as shown on MR images with a microelectrode in one of the recording positions for each area (Figure 1B). In a separate test, we measured the binocular eye traces (monkey Y only) when the animal was fixating an LED on the object at the two viewing distances (Supplementary Figure 1A). The difference in the horizontal eye position between left and right eye was clearly larger at the Near viewing distance compared to the Far viewing distance, indicating that the monkey converged correctly on the object at the two distances. The difference in vergence angle between the two viewing distances was also present in the monocular eye traces obtained during the recordings (Supplementary Figure 1B).

3.2 Apparatus and Recording procedures

During the experiments, the monkey was seated upright in a chair with the head fixed. Each animal was trained not to move the arm ipsilateral to the recorded hemisphere during the whole duration of the session. In front of the monkey, an industrial robot (Universal Robots, model UR-6-85-5-A) picked up the to-be-grasped object from a placeholder and presented it to the monkey. Four different objects (small plate 2.5 × 1 x 3.2 cm, large plate 5 × 2 x 6.5 cm, small sphere 2 cm diameter, large sphere 4 cm diameter) were pseudo-randomly presented one at a time in front of the monkey. Both plates were oriented at an angle of 30 deg from the vertical plane, therefore allowing the animals to keep the same hand orientation during their grasping. The object could appear either at a Near position (28 cm viewing distance, at chest level ~ 20 cm reaching distance measured from the center of the hand rest position to the center of the objects – peripersonal space) or at a Far position (56 cm – extrapersonal space – Figure 1B-C). The average object luminance were: large sphere 3.3 cd/m2; small sphere 11.2 cd/m2; large plate and small plate 3.4 cd/m2. Since both object size and viewing distance were exactly two times larger at the Far position compared to the Near position, the retinal size of a small object at the Near position and the same-shaped large object at the Far position was identical.

The objects required different types of grasping depending on their size, but comparable across monkeys: a pad-to-side grip (for the small sphere and the small plate), and a finger-splayed wrap, corresponding to a whole-hand grip (for the large sphere and the large plate – (Macfarlane and Graziano, 2009). Fiber-optic cables detected the resting position of the hand, the start of the reach to grasp movement, and the pulling of the object. The start of the hand movement was detected as soon as the palm of the hand was 0.3 cm above the resting plane, whereas pulling of the object was detected when the object was pulled for 0.5 cm in the horizontal axis.

We recorded single-unit activity with standard tungsten microelectrodes (impedance, 1 MΩ at 1 kHz; FHC) inserted through the dura by means of a 23-gauge stainless-steel guide tube and a hydraulic microdrive (FHC). Neural activity was amplified and filtered between 300 and 5000 Hz. Spike discrimination was performed online using a dual time-window discriminator and displayed with LabView and custom-built software. Spiking activity and photodiode pulses (corresponding to the onset of light in the object, see below) were sampled at 20 kHz on a DSP (C6000 series; Texas Instruments, Dallas, TX). We continuously monitored the position of the left eye with an infrared-based camera system (Eye Link II, SR Research), sampling the pupil position at 250 Hz.

3.3 Experimental Design and Statistical Analysis

The two monkeys were trained to perform two tasks in a dark room, a passive fixation (Fix trials) and a visually guided grasping (VGG, Grasp trials) task (Figure 1C). In Fix trials, the monkey had to passively fixate a small LED on the object which appeared either at the Near or at the Far distance until he received a juice reward. In Grasp trials, instead, he had to first fixate the LED on the object presented at the Near distance, and then, after a visual go cue (the offset of the LED on the object), to lift the hand from the resting position and pull the object in order to get the reward. Both types of tasks were performed using a robot, which picked one object at the time from a wooden placeholder, and presented it in front of the monkeys at one of the two distances. The fixation period was identical in the two types of trials (350-1500 ms).

To start both the Fix and Grasp trials, the monkey had to place the hand contralateral to the recording chamber in the resting position in complete darkness. During this time the robot picked an object from the box and moved it either to the Near or to the Far position. A red fixation LED inserted in the middle of the object was then illuminated, which the monkey had to fixate (keeping the gaze within a ±3.5 degrees – Monkey D – or ±5 degrees – Monkey Y – throughout the trial). After 500 ms, a white LED illuminated the object from within for a variable amount of time (350 - 1500 ms). If the red fixation LED did not dim until the end of the trial (Fix trials), the monkey's gaze remained inside the electronically defined window, and the hand remained in the resting position, the animal received a juice reward. In the other half of the trials, the red LED in the middle of the object dimmed (Go cue – Grasp trials), which was the signal for the monkey to lift his hand from the resting position, reach and pull the object for 300 ms (holding time) in order to obtain a reward. Note that when the object appeared at the Near position, the animal could not predict whether the trial would be a Fix trial or a Grasp trial up to the moment of the dimming of the red fixation LED.

All conditions (Fix Near, Fix Far and Grasp) were randomly interleaved in blocks of 10 trials per object type.

All data analysis was performed in Matlab (Mathworks). For each trial, the baseline firing rate was calculated from the mean activity recorded in the 300 ms interval preceding Light onset (white LED). For the Fix trials, we then calculated the net neural responses by subtracting the baseline activity from the mean activity observed between 40 and 600 ms after Light onset. We tested visual responsivity by means of t-tests ($p<0.05$) comparing the baseline activity to the activity in the period after Light onset. All neurons included in the current study were active in the Fixation task and in the VGG task.

For the Fix conditions, both cell-by-cell and population analysis were performed to quantify distance and object selectivity. For every responsive neuron, we computed a two-way ANOVA with factors *[distance]* and *[object] and* counted the number of cells with a significant main effect of distance, a significant main effect of object, or a significant *[distance x object]* interaction.

We plotted the averaged population net response to each object at the Near and at the Far distance, for each area. All the following statistical analyses were performed in two visual epochs, i.e. Early – from 40 to 200 ms after Light onset – and Late – from 200 to 400 ms.

We wanted to avoid the circularity in the analysis when the same data are being used for selecting and for testing (the double-dipping problem - Button, 2019). Therefore, we ranked the average net responses to the objects based on the odd trials at each distance (Near or Far) and separately for each area (test for significance in the two epochs – t-test $p<0.05$). Then, we plotted the average responses in the even trials based on this ranking. To test whether the object selectivity was similar at the two positions, we ranked the objects based on the responses at the Near distance and plotted the average responses to the same objects at the Far distance.

To assess distance selectivity, we first compared the average net response at the preferred distance (Best, i.e. the object eliciting the highest response in the test) to the average net response to the same object at the other distance (Worst). As in the previous analyses, we determined the preferred distance based on the even trials and plotted the responses in the odd trials. Then, to assess the preference of each area for a particular viewing distance, we compared the average net response to the preferred object presented at the Near position to the average net response to the same object at the Far position (test for significance in the two epochs – t-test $p<0.05$). The same analysis was also repeated selecting the preferred object at the Far position. Finally, to assess the neural selectivity for objects with identical retinal size, we compared the average net response to the best small object presented at the Near position to the average net response to the same shaped large object at the Far distance (test for significance in the two epochs – t-test $p<0.05$).

For Grasp trials in the light (VGG), we plotted the average response to the best object across all neurons per area, aligning the neural activity to multiple events during the trial (Light onset – Go cue – Lift – Pull). We measured the responsivity (t-test $p<0.05$) in each epoch of the trial by comparing the baseline firing rate to the activity in each epoch after the above-mentioned events. To test for differences in VGG activity between areas, we computed a two-way ANOVA with factors *[area]* and *[epoch],* the latter factor comprising an interval of 300 ms during object fixation and an interval of 300 ms after lift of the hand.

4. Results

Object and distance selectivity

All data included in this analysis were recorded in Fix trials, which were randomly interleaved with Grasp (VGG) trials. Since the results were highly similar between the two animals, we combined the data sets for all analyses, and provided the data separately for the two animals in Extended data. All neurons included (Monkey D: 45B, n = 57; F5a, n = 45; F5p, n = 44; Monkey Y: 45B, n = 57; F5a n = 44; F5p n = 32 – total number of neurons: 279) responded significantly to at least one object during fixation after Light onset. In each of the areas, we observed both Object- and Distance-selective neurons. The example neurons in Figure 2 illustrate the typical object (upper panel) and distance (lower panel) selectivity we observed in each of the areas. The example neuron of area 45B was clearly object-selective at the Near distance but not at the Far distance (two-way ANOVA, *object* x *distance* interaction, $F = 4.22$, $df = 3$, $p = 0.007$). In F5a, the object selectivity was generally weaker, and the responses evolved more slowly, as in the example neuron (middle column), whereas F5p neurons often showed transient responses to light onset with some object selectivity (right column). The lower panel of Figure 2 illustrates examples of distance selectivity in the three areas without clear object selectivity. The example neuron of 45B preferred the Near position (two-way anova main effect of distance, $p = 1.25 \times 10^{-24}$, $F = 168.73$, $df = 1$, $\eta = 2.79\%$), whereas the example neurons of F5a and F5p preferred the Far position.

The example neurons in Figure 2 also illustrate the different response profiles in the three areas. While area 45B neurons had a fast increase of the firing rate after light onset, neurons in area F5a showed a slower ramping up of the response without any brisk increase after light onset. Neurons in area F5p, instead, had an intermediate profile between 45B and F5a. To quantify the effects of Object, Distance and the interaction between these two factors, we performed a two-way ANOVA on the responses of each neuron. We observed a significantly higher proportion of object-selective neurons in area 45B compared to F5a and F5p (main effect of Object significant at $p < 0.05$ in 41% of the neurons in 45B, compared to 20% in F5a, $p = 7.4 \times 10^{-4}$; and 24% in F5p, $p = 6.21 \times 10^{-3}$, z-test). The proportion of neurons with a significant effect of Distance did not differ between the areas (45B: 44%; F5a: 36% and F5p: 38%, Supplementary Table 1. z-test for proportions, all p-values > 0.05).

To illustrate the object selectivity in each area, we ranked the objects for each selective neuron (selectivity was based on one-way ANOVAs, separately at the Near and at the Far positions) based on the responses in the odd trials and plotted the average response to the four objects in the even trials based on this ranking (Figure 3). In area 45B, we observed significant differences between preferred and non-preferred objects in the Early epoch (0-200ms) at both distances (one-way ANOVA, main effect of object $p = 3.05 \times 10^{-8}$, $F = 14.14$, $df = 3$, $\eta = 20.55\%$ and $p = 3.54 \times 10^{-4}$ $F = 6.75$, $df = 3$, $\eta = 17.41\%$ Near and Far, respectively, see Supplementary Table 2 for detailed statistics). In the Late epoch (200-400ms), instead, area 45B had a stronger object selectivity at the Near distance than at the Far ($p = 2.17 \times 10^{-9}$, $F = 16.44$ $df = 3$, $\eta = 23.13\%$, and $p = 0.03$ $F = 3.02$, $df = 3$, $\eta = 8.63\%$, respectively). Conversely, we did not observe comparable significant differences across objects in the other two areas (at the Near distance F5a was only significant during the late epoch $p = 3.5 \times 10^{-3}$ $F = 5.05$, $df = 3$, $\eta = 20.15\%$, while F5p was significant in the early epoch – $p = 3{,}1 \times 10^{-3}$, $F=5.40$, $df = 3$, $\eta = 26.82\%$; at the Far distance, $p>0.05$ at all-time epochs). A two-way ANOVA with factors [*object]* and *[area]* revealed that the object selectivity was significantly stronger in 45B than in the other two frontal areas, both at the Near ($p = 1.41 \times 10^{-5}$, $F = 11.40$, $df = 2$, $\eta = 3.87\%$) and at the Far ($p = 1.10 \times 10^{-6}$, $F = 11.66$, $df = 2$, $\eta = 4.03\%$) viewing distance.

To rule out the possibility that the object selectivity was induced by differences in eye movements between the four objects, we plotted the average horizontal position of the right eye for the four objects and the two viewing distances in Supplementary Figure 1B. In both monkeys, the eye position signal deviated slightly after Light onset (and more pronounced in monkey Y and at the Near viewing distance), which could be partially caused by the pupil's response to light onset. However, the eye traces were very similar across the four objects in our experiment (all differences were less than 0.6 deg in monkey D and less than 1 deg in monkey Y.

Next, we investigated the effect of viewing distance by first determining the preferred viewing distance for every neuron. Contrary to our expectations, we observed significantly more neurons preferring the near distance in area 45B (58%) and in area F5a (55%) than in F5p (39%, $p = 5.1 \times 10^{-3}$ and $p = 0.02$, z-test; Supplementary Table 3). Thus, the majority of F5p neurons preferred the Far distance. Then, to quantify the strength of the distance selectivity, we compared the average net response to the preferred object at the Best distance to the response to that same object at the Worst distance (Figure 4 and Supplementary Figure 2). We first calculated two-way ANOVAs with factors *distance* (near – far) and *epoch* (early – late) for each area separately. All three areas had a significant main effect of distance, only 45B had a significant main effect of epoch, and only F5a showed a significant interaction between distance and epoch (Supplementary Table 4). For area 45B and F5a, the effect of distance was significant both in the early and in the late epoch (t-test, df = 113: $p = 1.98 \times 10^{-7}$ and $p = 3.62 \times 10^{-9}$, respectively early and late epoch in 45B; df = 88: $p = 4.49 \times 10^{-4}$ and $p = 2.30 \times 10^{-4}$, respectively early and late epoch in F5a) while area F5p only showed a significant effect of distance in the late epoch (df = 75: $p = 3.82 \times 10^{-4}$, See Supplementary Table 4). Averaged across neurons and across the entire stimulus presentation interval, frontal neurons responded 79% (45B), 55% (F5a) and 74% (F5p) less to the preferred object at the worst distance compared to the same object at the best viewing distance.

Viewing distance may not only affect the responses to the preferred object, but also the object preference of the neuron. In other words, is the object selectivity invariant across viewing distance? We first ranked the objects based on the average response of each neuron at the Near position, and then calculated the response to the same objects at the Far position. The average neuronal tuning for objects at the Near distance was stronger in 45B than in the other two areas: the slope of the regression line for area 45B was -3.71, for area F5a the slope was -2.65, and for F5p the slope was -2.45 spikes/sec/stimulus rank (Figure 5, Supplementary Figure 3 and Supplementary Table 5). However, in every area the object preference was only weakly preserved at the Far distance. The slopes of the regression lines at the Far position were -0.81 in 45B, -0.40 in F5a, and -0.35 in F5p, all of which were significantly different from the slope at the Near distance (Supplementary Table 5 for confidence intervals). Thus, neurons in these three areas are sensitive to changes in the viewing distance of an object.

Because the viewing distance affected the object preference in all three areas, we determined the preferred object according to the highest response at the Near location and compared this to the response to the same object at the Far position (Figure 6A, Supplementary Figure 4 and 5), and vice versa (preferred object based on the Far location, Figure 6B, Supplementary Figure 4 and 5). When selecting the preferred object based on the Near location (Figure 6A), area 45B and area F5a showed a strong effect of viewing distance in both early and late epochs (45B: early and late epochs, t-tests, $df = 113$: $p = 6.55 \times 10^{-5}$ and 3.98×10^{-7}, respectively; F5a: $df = 88$: $p = 3.00 \times 10^{-3}$ and $p = 1.17 \times 10^{-5}$, respectively; See Supplementary Table 6). Unexpectedly, F5p had a relatively weak Near preference in the early epoch ($df = 75$, $p = 3.50 \times 10^{-3}$), and no effect of viewing distance in the late epoch ($p > 0.05$ – Figure 6A). When selecting the preferred object based on the Far location (Figure 6B), we observed a weak effect of viewing distance in 45B, which was much smaller than when selecting based on the Near responses (two-way ANOVA, interaction effect between the *Selected distance for ranking* and *Distance,* $p = 6.70 \times 10^{-3}$ $F = 7.41$, $df = 1$, $\eta = 1.56\%$). In F5p, however, the viewing distance effect was much stronger (two-way ANOVA, $p = 0.01$, $F = 6.08$, $df = 1$, $\eta = 1.93\%$), consistent with the higher proportion of Far preferring neurons. F5a showed an intermediate pattern of distance selectivity, since we measured a moderate effect of viewing distance when selecting based on the Near ($df = 88$, $p = 5.05 \times 10^{-5}$, t-test) or Far ($df = 88$, $p = 3.03 \times 10^{-4}$, t-test) responses, but a non-significant interaction effect between the factors *Selected distance for ranking* and *Distance* ($p = 0.80$, $F = 0.06$, $df = 1$, $\eta = 0.018\%$).

Presenting the same object at the two positions also introduces a change in retinal size (Figure 1C), which may influence the neuronal responses. To investigate the effect of viewing distance for objects with identical retinal size, we compared the average net responses to the small object at the Near distance with those to the same shaped large object at the Far distance Figure 7 and Supplementary Figure 6). Only area 45B and F5a preserved a significant preference for the Near position during the Late epoch (t-test, df = 113, $p = 6.40 \times 10^{-3}$ and df = 88, $p = 1.80 \times 10^{-3}$, respectively), but not in the Early epoch (df = 113, p = 0.23 for 45B and df = 88, p = 0.07 for F5a). In contrast, F5p neurons did not distinguish between these two conditions in none of the epochs (t-test, df = 75, p = 0.07 and p = 0.45 for Early and Late epoch, respectively). Therefore, for stimuli with identical retinal size, 45B and F5a neurons preserve their preference for the Near viewing distance, while F5p neurons show no clear preference anymore under these conditions.

Grasping activity

We also recorded during visually guided grasping (VGG) of the same objects, interleaved with Fixation trials at the Near viewing distance. To guarantee that the animals could not predict whether a trial would be a Fixation trial or a Grasping trial, Fixation trials were rewarded at the same time (350-1500 ms after Light onset) when the go-cue would appear in Grasping trials. We verified that there were no significant differences in neuronal responses between Fixation trials and the object fixation epoch of Grasping trials in any of the areas (all p values > 0.1, data not shown).

The majority of neurons that responded to Fix trials after Light onset, also responded in at least one epoch after Light onset in the grasping trials (Supplementary Table 7). Figure 8A-B-C shows the average response to the best object aligned to Light onset, Go cue, Lift of the hand and Pull, respectively, in the VGG task (grasping in the light, Supplementary Figure7). Area 45B (N = 114) and F5a neurons (N = 89) showed a response to Light onset, and a sustained response throughout the delay period and during the Pull of the object. In area F5p (N = 76), instead, we observed a transient response to Light onset, followed by a decrease in activity 200-300 ms after Light onset.

A two-way ANOVA with factors *[area]* and *[epoch]* (i.e., 300 ms during object fixation and 300 ms after lift of the hand) showed a significant interaction (F = 8.83, df = 2, $p = 1.67 \times 10^{-4}$, η

= 3.09%) and epoch ($F = 1.85$, $df = 1$, $p = 1.67 \times 10^{-2}$, $\eta = 1.00\%$), but no significant effect of area ($F = 1.85$, $df = 2$, $p = 0.16$, $\eta = 0.65\%$), indicating that the three areas responded differently in the VGG task. Around the Lift of the hand, the F5p activity rose strongly (t-test on the interval [-300-0] ms before the lift of the hand compared to [0-300] ms after the lift of the hand, $df = 11$, $p = 5.80 \times 10^{-3}$). Moreover, F5p neurons were significantly more active after the lift of the hand compared to the object fixation epoch ([0-300 ms after lift of the hand compared to the interval [0-300] ms after Light on, t-test: $df = 76$, $p = 3.51 \times 10^{-5}$). In contrast, area 45B was more active during the object fixation period (Light on), than during the Lift of the hand (t-test: $df = 113$, $p = 1.26 \times 10^{-2}$), whereas F5a was equally active during object fixation and lift of the hand ($df = 87$, $p = 0.16$). Thus, all three areas were highly active during visually-guided object grasping, but only F5p showed a strong increase in activity around the lift of the hand.

We investigated the differences in activity in the VGG task between Near preferring and Far preferring neurons in the three areas. We plotted the activity in the VGG task separately for the two types of neurons (Figure 8D). In area 45B and F5a, the VGG activity was very similar in Near and Far preferring neurons (no significant differences in any epoch of the trial). However, Near preferring neurons in F5p showed much stronger enhancement of activity around the lift of the hand compared to Far preferring neurons, suggesting a more prominent role in motor planning and execution (as in movement neurons in the FEF, see [23]. Indeed, the average activity [200-300 ms] after the lift of the hand was significantly higher than the activity [-300 to -200 ms] before the lift of the hand in Near preferring neurons ($p = 6.00 \times 10^{-3}$), but not in Far preferring neurons ($p = 0.07$).

5. Discussion

Neurons in area 45B, F5a and F5p responded to the presentation of the object and were selective for viewing distance, but only 45B neurons were selective for both object and viewing distance. Contrary to our expectations, we observed a strong preference for the Near viewing distance in 45B and F5a and a preference for the Far viewing distance in F5p. Even for objects with identical retinal size at the two viewing distances, 45B and F5a neurons preferred the Near viewing distance. These results suggest that both area 45B and F5a may play a role in visually guided object grasping.

The source of the distance selectivity we observed cannot be easily determined from our experiments. Vertical disparities can be a source of visual information about distance, but only for relatively large stimuli (covering more than 10 deg [24]). Since our largest objects were only 12 deg in diameter, vertical disparities are an unlikely source for distance in our study. Vergence angle, in contrast, clearly covaried with object distance and could therefore be used to inform the frontal areas about the object's position in space. However, we cannot exclude the possibility that our animals also used other cues such as the position of the robot arm to estimate object distance.

The neural coding of viewing distance has been studied in early visual areas [25], in dorsal [26-28] and in ventral stream areas in nonhuman primates [29]. However, very few studies have investigated the neural coding of distance in the context of a reaching or grasping task. [30] investigated the effect of binocular eye position in rostral parietal area PE on the reaching-related activity of individual neurons and reported that a small subpopulation of neurons was influenced by viewing distance. [14,15] described joint selectivity for fixation distance and reach direction in the caudal parietal area V6A. In these studies, the fixation distance varied within the peripersonal space of the animal (i.e. less than 25 cm from the animal), and therefore no data were obtained for targets that appeared beyond reaching distance.

Area 45B neurons showed fast and selective visual responses to the object after Light onset. Previous studies described fMRI activations in this area evoked by 2D images of objects [31,32] ,and selectivity of individual neurons for shapes and very small line fragments [12], and zero order disparity [10]. We confirmed the involvement of these neurons in shape and object processing during grasping. Most 45B neurons were also significantly affected by viewing distance and showed a preference for Near even when correcting for retinal size. Our hypothesis was that neurons that encode objects in purely visual terms should not be affected much by the distance manipulation (for identical retinal size), while neurons in which the object response primarily represents the motor plan would respond less to objects that cannot be grasped (i.e. in the far trials, again keeping the visual input identical by presenting a larger object at the far distance). However, we observed the opposite effect: neurons in the more 'visual' area 45B preferred the near viewing distance whereas the more 'motor' area F5p showed a slight preference for the far presentations. This observation – together with their strong responses during visually-guided object grasping – is compatible with the idea that area 45B neurons are important for processing object information during grasping.

Because of the visual properties of this area and the direct anatomical connection with pAIP [9], we previously hypothesized that area 45B could be involved in oculomotor control, similar to the neighboring region FEF [12,33], to guide eye movements towards specific parts of the object contour. However, we observed sustained object responses in a visually-guided grasping task, which do not seem to be consistent with pure oculomotor control since no saccade was required after obtaining fixation. Our results rather suggest that area 45B may have a role in object processing and eye-hand coordination when grasping objects under visual guidance. The strong distance selectivity with a preference for Near was also inconsistent with our initial hypothesis, and could not be explained as a vergence effect, as the eye position was stable after light onset. At least for the subpopulation of neurons preferring the peripersonal space, we cannot exclude the possibility that the distance effect we observed was related to the significance that the stimulus acquired when it was reachable, and therefore graspable. Our results are in accordance with [20], who reported activations in prefrontal cortex in response to object presentation at reachable distances.

The F5a results were largely consistent with the known anatomical connectivity and neuronal properties of this area. Although we measured significant object selectivity in individual F5a neurons, our population of F5a neurons was only weakly object-selective, most likely because we only used a limited number of objects. Nevertheless, the F5a neurons we recorded were strongly affected by viewing distance, preferring the Near viewing distance even for stimuli with identical retinal size. Overall, these properties are consistent with the proposed position in the cortical hierarchy as 'pre-premotor cortex' [33], receiving visual inputs from AIP and transmitting information to F5p. Note that - in contrast to F5p neurons – 45B and F5a neurons with different distance preferences behaved similarly in the VGG task, which may be related to the primarily visual character of the responses in these two areas.

Previous studies have described the connectivity pattern of F5p as strongly motor-oriented, receiving input from F5a and projecting directly to primary motor cortex [13,34]. Being part of the same pathway (pAIP → aAIP → F5a → F5p), several authors comparing object representations in AIP and F5p [4,11] concluded that AIP provides a visual object description, while area F5p represents the same object in motor terms, i.e., the grip type necessary to grasp the object. In our study, Near preferring F5p neurons showed stronger peri-lift modulation than Far preferring neurons, suggesting a more prominent role in motor planning and execution of these neurons. [35] reversibly inactivated F5 (probably F5p) with muscimol, which induced a deficit in the preshaping of the hand during grasping. Because objects may be encoded in motor terms in F5p, we hypothesized that F5p would strongly prefer the Near distance but unexpectedly, a high number of neurons preferred the Far viewing distance. Our results seem to be in contrast to [20], reporting Near preference in F4/F5p area. However, the 'Far space' distance for object presentation in [20] was significantly larger than in our case (150 cm and 56 cm, respectively). Therefore, it is possible that our Far viewing distance was not long enough to reduce the visuomotor neural responses in F5p. Another difference with our study is that [20] analyzed fMRI responses in monkeys, which may also include subthreshold modulations and presynaptic activity [36] .

Our results are important for the interpretation of the organization of the parieto-frontal grasping network. In pAIP, visual information is transmitted along two parallel pathways: towards aAIP, and then to F5a and F5p, and directly to 45B [9] . The fact that 45B neurons preferred objects in peripersonal space even after equating retinal size, together with its direct input from posterior AIP, suggests that this area may also play a role in object processing during visually-guided object grasping. Recently, we showed that area 45B is causally related to object grasping using reversible inactivations [37], suggesting that eye-hand coordination (monitoring the position of the own hand approaching the object) may be supported by 45B neurons.

Our data suggest a much more complex role of 45B in the network rather than directing saccades towards object contours. The strong visual responses and the surprising preference for the Far viewing distance of area F5p suggest that the visuomotor object representation in F5p was still activated when we presented objects beyond reaching distance. The presence of a transparent barrier interposed between the monkey and the object could have decreased or silenced the F5p response to objects located both at the Near and Far distances in a similar way as in [16] .

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The study is reported in accordance with ARRIVE guidelines.

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Author contribution

PJ and IC designed the experiment; IC collected the data and analyzed the data; PJ and IC wrote the paper.

Figures legends

Figure 1. Anatomical location of areas of interest and eye traces. A. Schematic view of a macaque brain (edited from the 'Scalable Brain Atlas' http://link.springer.com/content/pdf/10.1007/s12021-014-9258-x; Calabrese et al 2015). Colored dots represent the areas of interest in the arcuate sulcus, respectively Area 45B – blue, Area F5a – red – and Area F5p - green. B. Anatomical electrode recording position in Monkey D. Yellow arrows indicate the electrode tip location in the three areas. Equivalent recording positions in Monkey Y were reported (data not shown). C. Schematic representation of the behavioral task, stimuli and distances. The first block represents the common events to both Fix and Grasp tasks. The right-upper block corresponds to Fix task, the right-lower represents the Grasp task. Objects: large and small spheres and plates (oriented at 30° from the vertical plane – y-axis; plates size: 5 × 2 cm and 2.5 × 1 cm, respectively). Two viewing distances (Near, Far) from the monkey's eyes. See details in the text.

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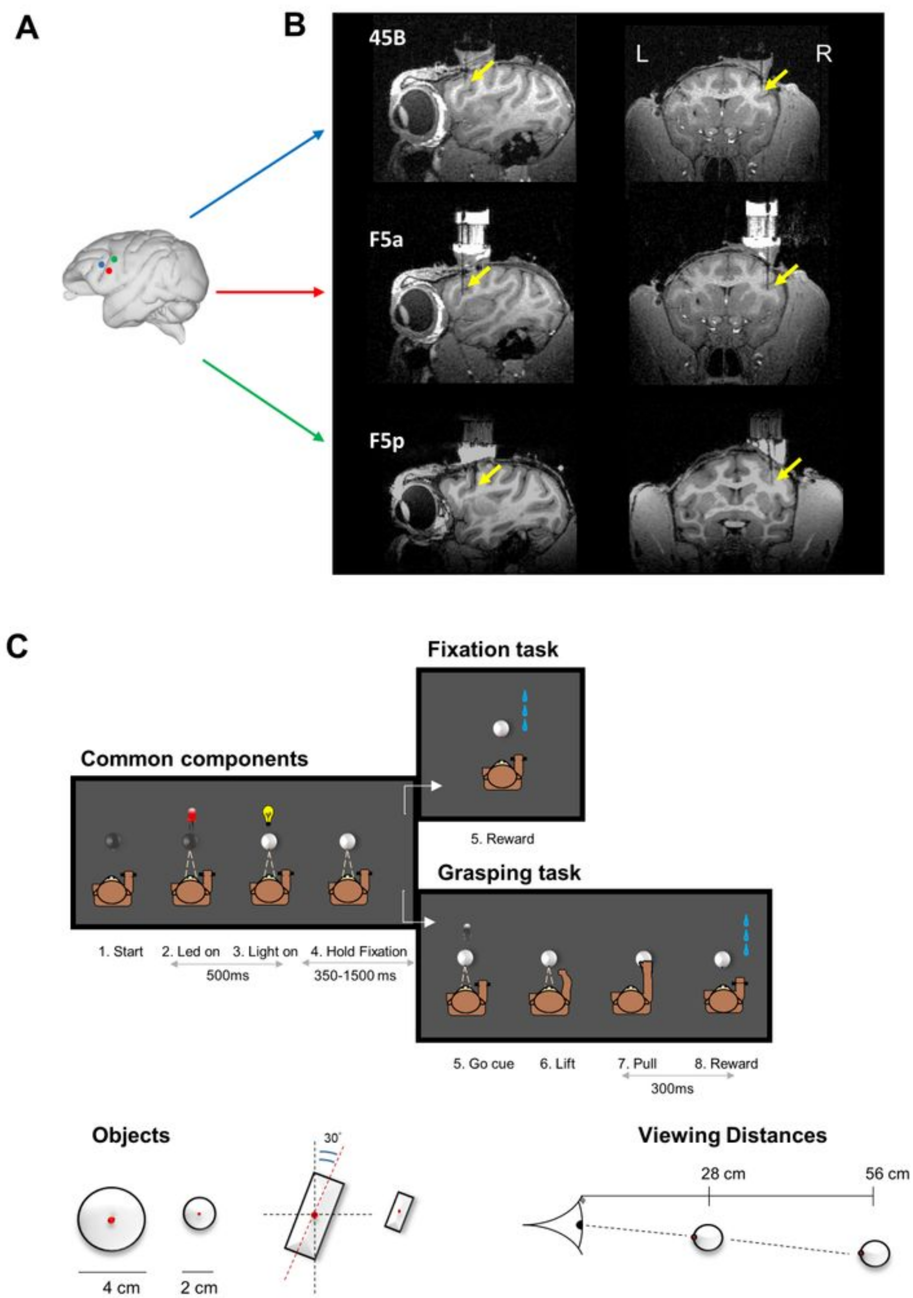
Figures

Figure 1



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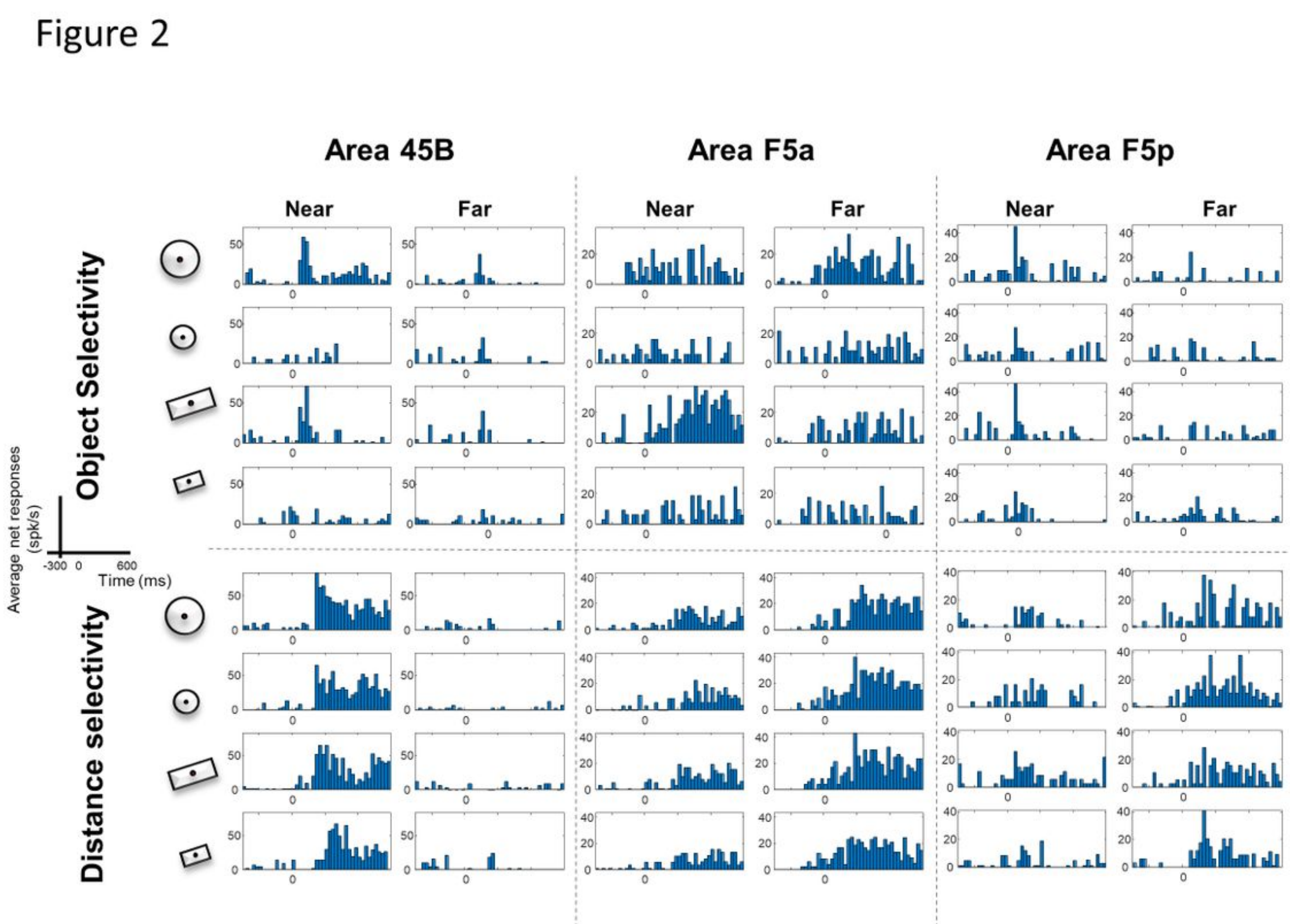

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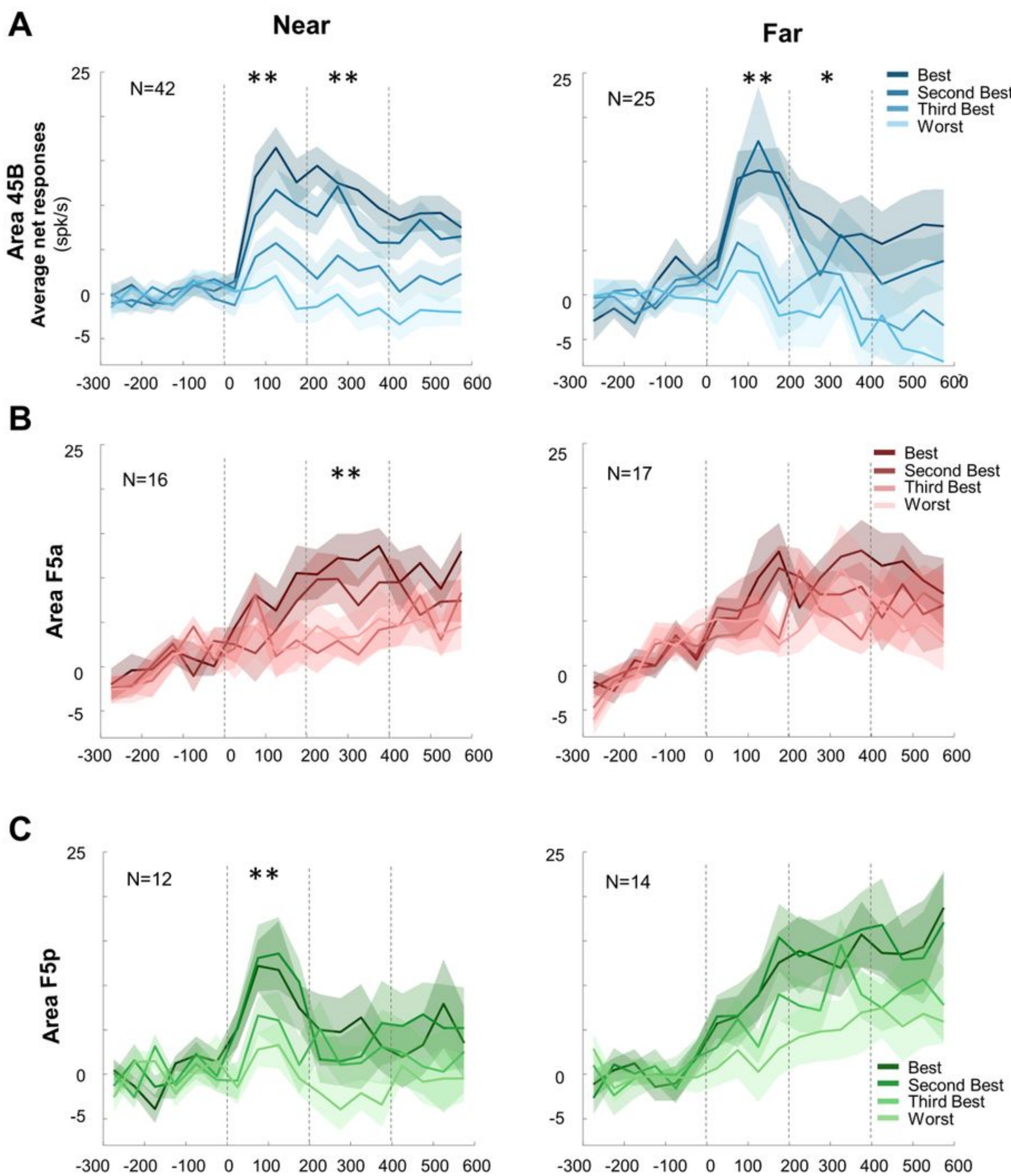

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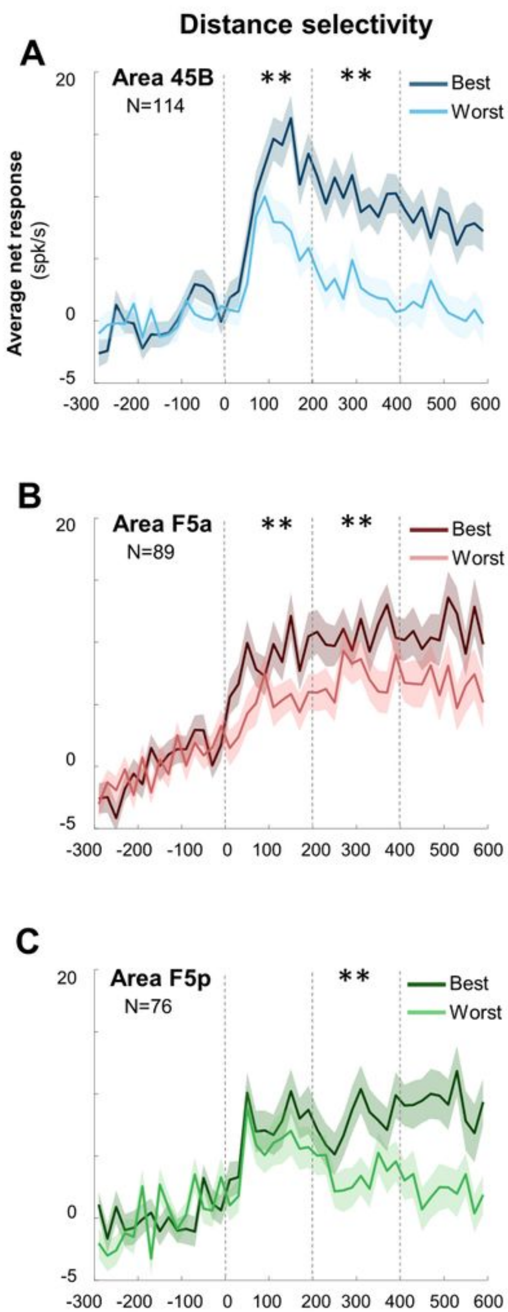

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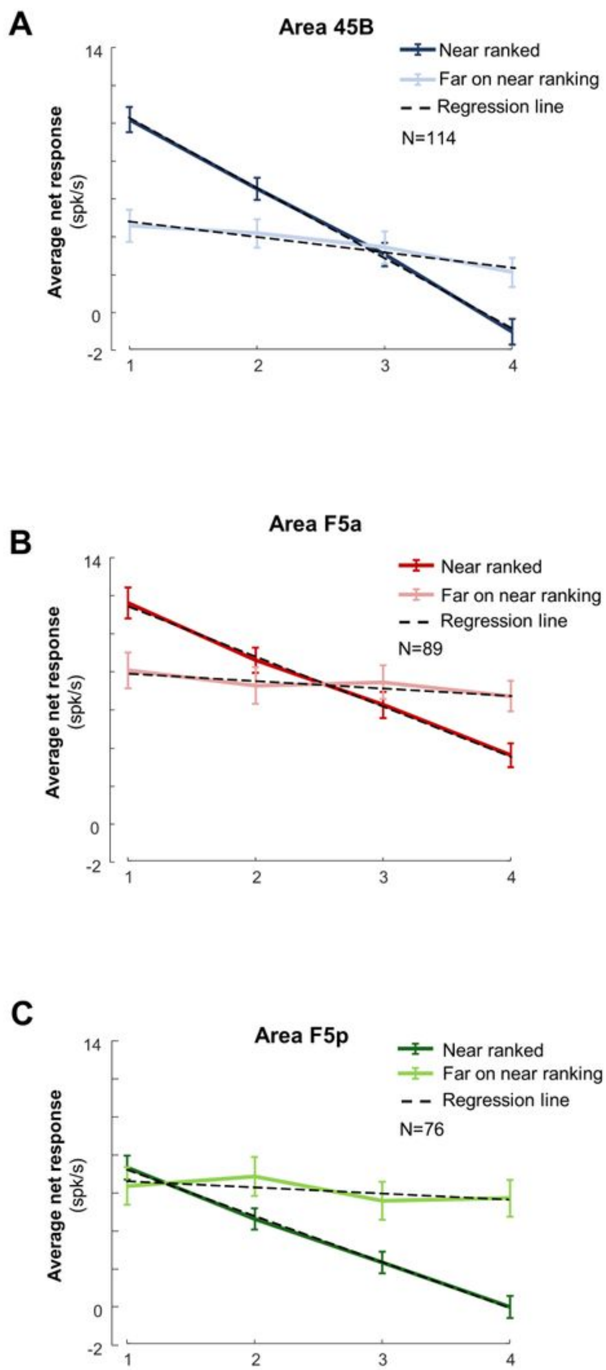

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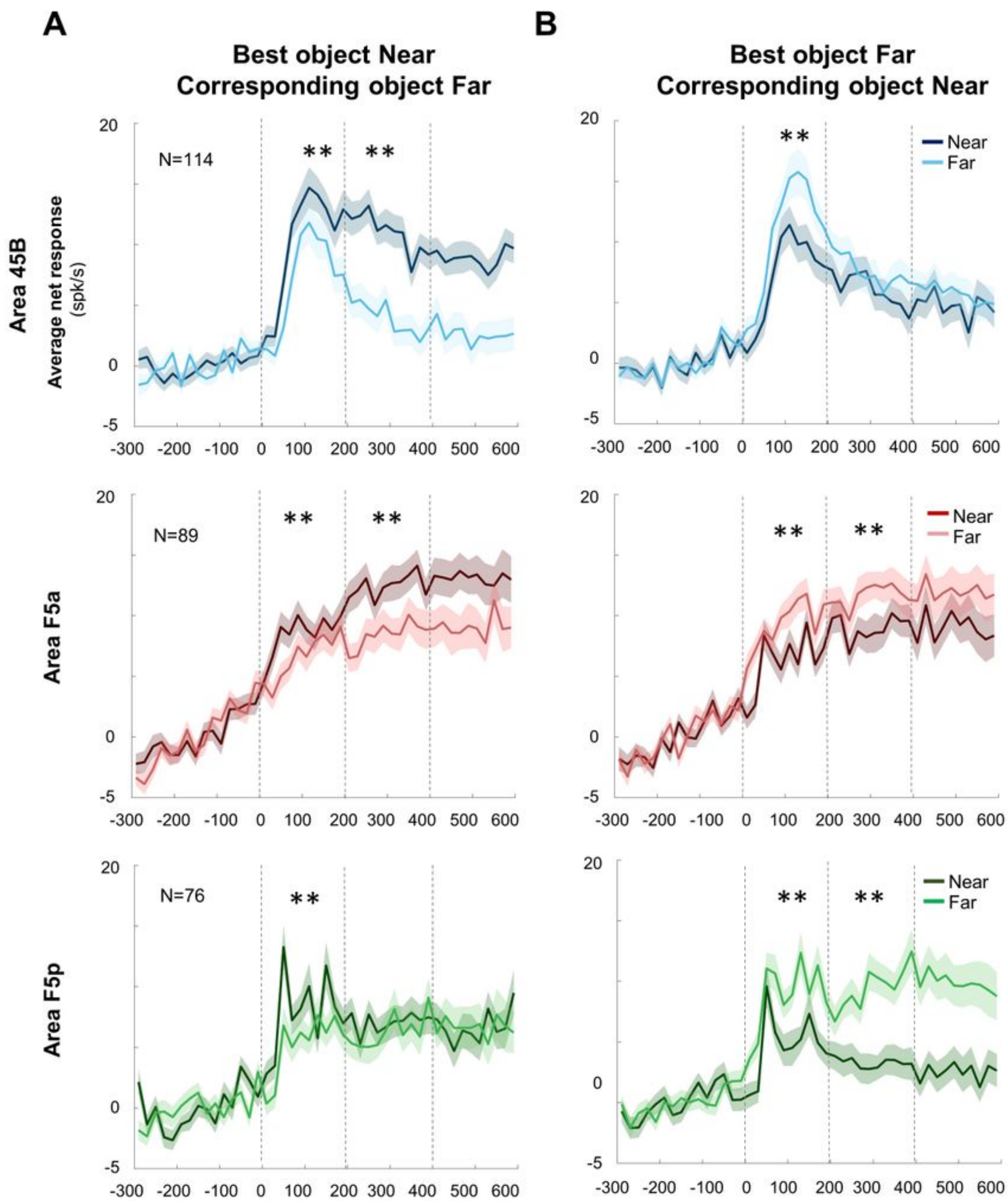

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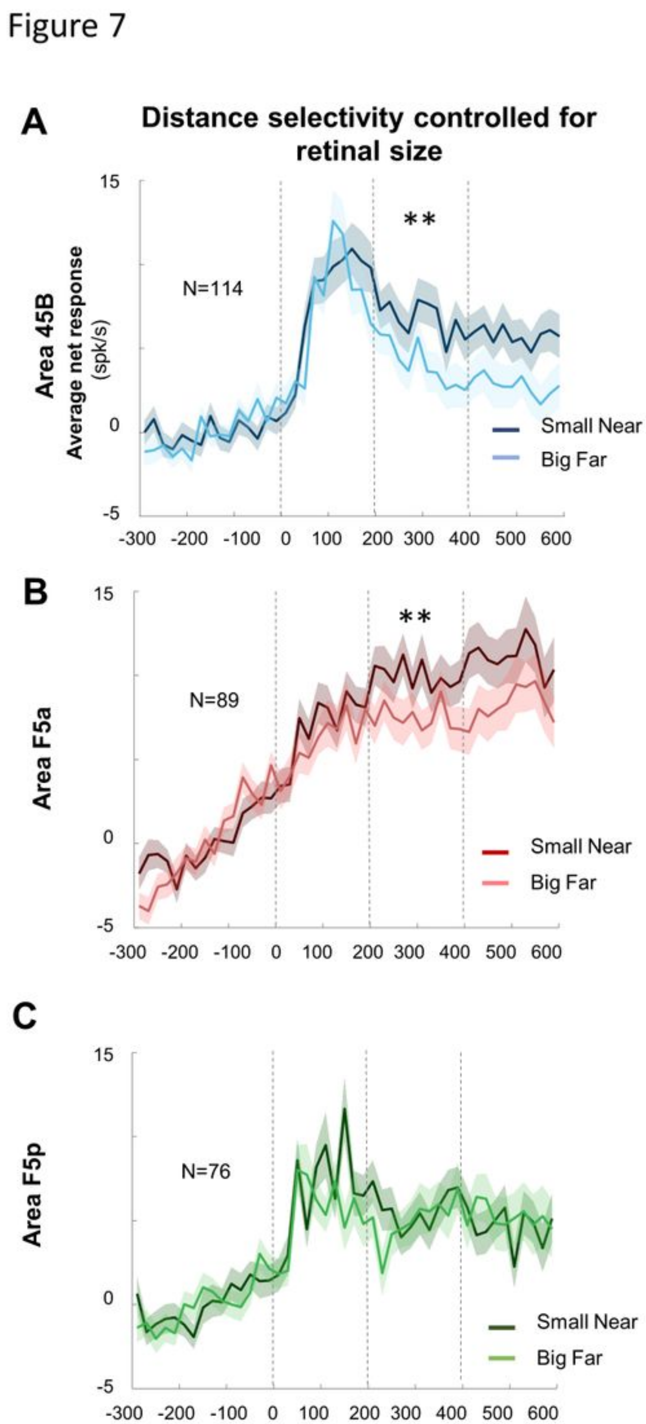

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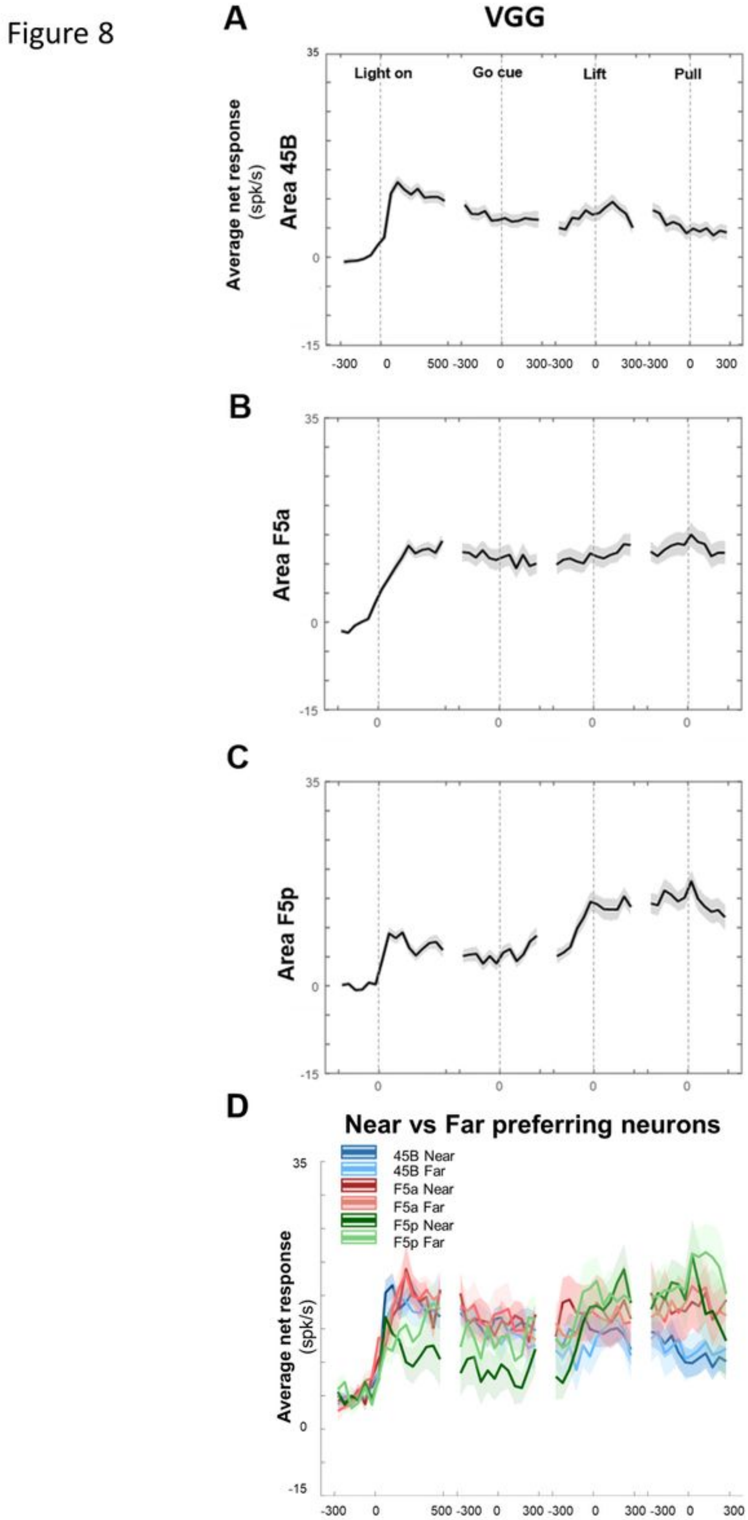

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