When is the earliest neural response to faces in the occipital face area?

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Single case studies of neuropsychological patients have been used to constrain neural models of cognitive function. In this tradition Rossion reports how studies of acquired prosopagnosic patient P.S. informed his model of the face processing network (Rossion, 2022). Rossion discusses the role of the occipital face area (OFA) and what he argues are conclusions that are inconsistent with our transcranial magnetic stimulation (TMS) studies. I address these differences here.

The face recognition deficits exhibited by P.S. (Rossion et al., 2003) suggested that the OFA is necessary for visual face recognition. To further explore this, we used TMS to disrupt the OFA while participants discriminated faces in which we manipulated face parts (the eyes and mouth), or the spacing between these parts (Pitcher et al., 2007). Results showed that TMS disrupted only face part discrimination and that it did so when double-pulse TMS was delivered at 60-100ms. The early latency was temporally discrete in that TMS delivered at other latencies (20-60ms, 100-140ms, 130-170ms, 170-210ms and 210-250ms) had no effect.

Rossion argues that 60-100ms is too early to reflect a genuine signal of face processing because the OFA is functionally active only after the fusiform face area (FFA) (Figure 1). I disagree and have suggested that TMS is likely to disrupt task performance at latencies that precede face-selective responses recorded from the scalp that peak at 100ms and 170ms (Pitcher, 2022). We demonstrated this experimentally in a study where TMS delivered over the OFA at 60-100ms selectively increased the N170, the neural response to faces that peaks 170ms after stimulus onset (Sadeh et al., 2011). It is also consistent with a macaque microstimulation study reporting a face-selective local field potential (LFP) response peaking at 150ms in the temporal lobe (Afraz et al., 2006). Crucially, the greatest impairment in face detection accuracy was observed when microstimulation was delivered at the early latency of 50-100ms and not at the later latency at 100-150ms that overlapped with the LFP peak at 150ms. I suggest that disrupting task performance (with TMS or microstimulation) is most effective when the neural activity that supports task performance is building. By contrast, the peak of neural activity (as measured with MEG or LFP) represents neural activity that has already occurred, and any stimulation to disrupt task performance will be less effective or simply too late (Pitcher, 2022).

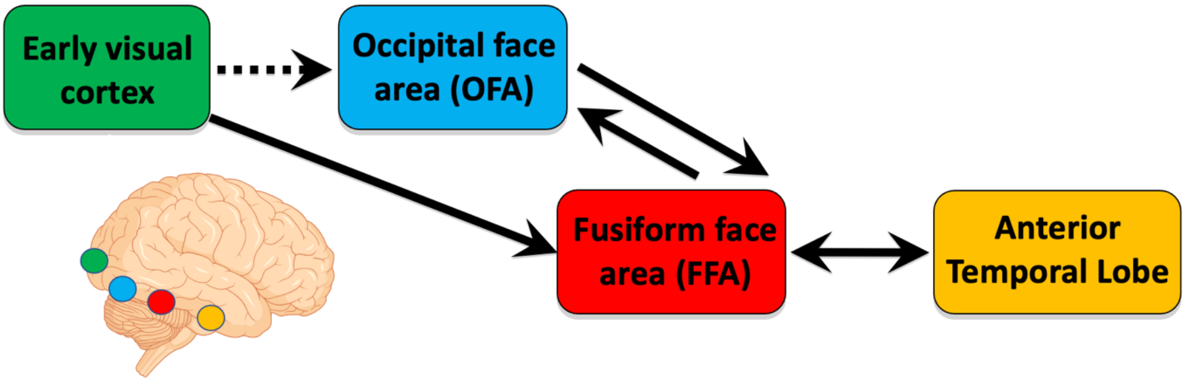

Figure 1. Rossion's model of the cortico-cortical connections between the brain areas necessary for visual facial identity recognition (adapted from Figure 6 in Rossion, 2022). Rossion argues that the direct connection between early visual cortex and the OFA (denoted by a dotted line) may not result in a face preferential response. This is inconsistent with data showing that double pulse TMS delivered at 60-100ms over the OFA impairs a face part discrimination task (Pitcher et al., 2007). I argue it is implausible that the connection between early visual cortex and the OFA is not essential for a range of face processing tasks, including identity recognition. In addition, I propose that all the cortico-cortical connections between the four areas in the model should be bi-directional.

This still leaves open the question of precisely when the OFA and the FFA exhibit the initial neural response in a facial identity recognition task. A later TMS study (Pitcher et al., 2012) with more precise temporal resolution demonstrated that the OFA was face-selective at approximately 100ms (but the latency varied across participants). This result, along with MEG data (Itier et al., 2006) suggests the initial response to faces in the OFA peaks at approximately 100ms. Unfortunately, TMS cannot address the latency of the FFA response as the FFA is outside the range of effective stimulation.

Because P.S. lacks a right OFA Rossion argues that the FFA is functionally active before the OFA, despite the OFA being closer to early visual cortex (Figure 1). I agree that the OFA and FFA may respond to faces at a similar latency (say within 10ms of each other). However, it seems less plausible that the face information represented in the OFA remains unused until feedback mechanisms from higher cortical areas require this information as Rossion suggests. It also seems likely that any feedforward and feedback mechanisms between the OFA and FFA will change depending on the face tasks being performed (e.g., identity or expression recognition). For example, in our TMS studies the face parts (e.g., eyes, nose and mouth) are manipulated to produce subtle physical differences in a face, rather than in the perception of an entirely different identity (Pitcher et al., 2012; Pitcher et al., 2007). Perhaps these differences in task can account for the theoretical differences between us.

Rossion further suggests that the neural disruption induced by TMS is not necessarily restricted to the brain area that is being directly stimulated. I agree, while noting it is not possible to make this claim in a TMS behavioural experiment where the only measure of disruption is the reduction in concurrent task performance (Pitcher et al., 2012; Pitcher et al., 2007). We combined thetaburst TMS (TBS) with neuroimaging to show that TBS delivered over the OFA reduced the BOLD response to faces (and non-face stimuli) in remote brain areas including the FFA (Pitcher et al., 2014). However, the technical challenges of combining methods prevented the collection of behavioural task data. It is therefore possible that the observed neural reductions in the OFA and FFA may not have impaired behavioural performance. This is an important question and needs to be addressed in future studies.

The question of TMS site localisation is also raised by Rossion as a limitation of our study (Pitcher et al., 2007). At the time we did not have access to individual functional face localisers for participants and used group MNI coordinates co-registered to individual structural scans. Rossion claims this is problematic because the coordinates we used from his study (Rossion et al., 2003) did not accurately represent the individual variations in OFA location. However, the criticism is severely weakened by our control experiment in which stimulation of the object-selective lateral occipital area (LO) did not impair face part discrimination (LO is approximately 1-2cm from the OFA). In addition, differences in site localisation methods have been shown to have no qualitative differences in observed TMS behavioural impairments. For example, the effect sizes in a TMS study of scene perception that used mean MNI coordinates for site localisation were comparable to the effect sizes from a prior study that used individual functional localisers (Wischnewski & Peelen, 2021).

In conclusion, Rossion's detailed studies of P.S. have undoubtedly enhanced understanding of face processing. However, his criticisms of TMS do not bear scrutiny and these studies should be used alongside neuropsychological patient data to investigate causal disruption in the face network.

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