Behavioral/Systems/Cognitive

Cortical Dynamics Underlying Face Completion in Human Visual System

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In natural images, visual objects are typically occluded by other objects. A remarkable ability of our visual system is to complete occluded objects effortlessly and see whole, uninterrupted objects. How object completion is implemented in the visual system is still largely unknown. In this study, using a backward masking paradigm, we combined psychophysics and functional magnetic resonance imaging to investigate the temporal evolvement of face completion at different levels of the visual processing hierarchy. Human subjects were presented with two kinds of stimuli that were designed to elicit or not elicit the percept of a completed face, although they were physically very similar. By contrasting subjects' behavioral and blood oxygenation level-dependent (BOLD) responses to completed and noncompleted faces, we measured the psychophysical time course of the face completion and its underlying cortical dynamics. We found that face completion manifested its effect between 50 and 250 ms after stimulus onset. Relative to noncompleted faces, completed faces induced weaker BOLD response at early processing phases in retinotopic visual areas V1 and V2 and stronger BOLD response at late processing phases in occipital face area and fusiform face area. Attending away from the stimuli largely abolished these effects. These findings suggest that face completion consists of two synergetic phases: early suppression in lower visual areas and late enhancement in higher visual areas; moreover, attention is necessary to these neural events.

Introduction

Great strides ha e been made in nderstanding the ne ral mechanisms of is al object recognition (Grill-Spector and Malach, 2004; Kan isher, 2010). So far, object recognition has been st died mainl sing indi id al objects presented alone. Ho e er, is al objects rarel occ r in isolation in nat ral scenes. It is common for one object to occl de another object in nat ral images. A striking abilit of h man ision is the recognition of objects e en hen the sensor information specif ing objects is opticall incomplete d e to occl sion. We ha e little diffic lt completing occl ded objects and seeing hole, ninterr pted objects.

Ho object completion is implemented in the is al corte remains el si e. E idence from h man brain imaging st dies s ggest that (onl) high-le el is al areas selecti e for objects are likel candidates to mediate the operation of object completion effects (Doniger et al., 2000; Lerner et al., 2002; Stanle and R bin, 2003; Hegdé et al., 2008; Gr tzner et al., 2010). Ho e er, ps choph sical and electroph siological st dies s ggest that earl is al cortical areas also pla an important f nctional role in object completion (Naka ama et al., 1989; S gita, 1999; Bakin et al., 2000; Pillo and R bin, 2002). The discrepanc co ld be d e to sl ggish temporal response of the f nctional magnetic resonance imaging (fMRI) method. In the fMRI st dies b Lerner et al. (2002) and Hegdé et al. (2008), occl ded objects ere presented for h ndreds of milliseconds. This completion-related acti ation in object-selecti e areas as detected b fMRI might ha e reflected the percept al conseq ence of object completion, rather than the process of object completion.

Ps choph sical and e ent-related potential (ERP) st dies ha e sho n that object completion is not instantaneo s; instead, it manifests its effect ithin a temporal indo shortl after stim l s onset (Sek ler and Palmer, 1992; M rra et al., 2001; Johnson and Olsha sen, 2005; Chen et al., 2009). In this st d , e attempted to in estigate the temporal e ol ement of face completion at different le els of the is al hierarch . To circ m ent the lo temporal resol tion deficit of the fMRI method, e sed a back ard masking paradigm to present occl ded faces ith ario s d rations, hich rendered it possible to interr pt the is al processing of occl ded faces and follo in some detail the temporal e ol ement of face completion (Grill-Spector et al., 2000; Bar et al., 2001; Lamme et al., 2002).

Vis al stim li ere constr cted b presenting identical face fragments stereoscopicall either behind or in front of a te t red occl der (Fig. 1). In the first condition, the stim li ere percept all completed and organized into a coherent face. In the second condition, the ere percei ed as disjoint face fragments ho ering abo e the te t red occl der (Naka ama et al., 1989;

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T a pp d b Na a Na a Sc c F da f C a (P j c 30870762, 90920012, a d 30925014), F da a R a c F d f C a U , M f Sc c a d T c f C a (2005CB522800, 2004CB318101, a d 2010CB833903), a d K d I a P a f C Acad f Sc c .

C p d c d b add d Fa Fa , D pa f P c a d K Lab a f Mac P c p (M f Ed ca), P U , 5 Y a R ad, B j 100871, P p ' R p b c f C a. E- ff a @p . d .c .

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Fang and He, 2005). In the ps choph sical e periment and the first fMRI e periment, b contrasting s bjects' beha ioral and blood o genation le el-dependent (BOLD) responses in these t o conditions, e meas red the ps choph sical time co rse of the face completion and its nderl ing cortical d namics. In the second fMRI e periment, e in estigated the role of attention in the face completion. The third fMRI e periment as performed to r le o t alternati e e planations to the data in the first e periment.

Materials and Methods

S . Eight h man s bjects (6 female and 2 male) participated in the ps choph sical and the first t o fMRI e periments. Fo r of them (3 female and 1 male) participated in the third fMRI e periment. All of them ere right-handed, reported normal or corrected-to-normal i-sion, and had no kno n ne rological or is al disorders. Ages ranged from 19 to 33 ears. The ga e ritten, informed consent in accordance ith the proced res and protocols appro ed b the h man s bjects re-ie committee of Peking Uni ersit .

S . Face stim li in the ps choph sical and the first t o fMRI e periments ere identical, hich s btended 10.6 × 10.6 of is al angle and ere presented against a gra back-gro nd. Occl ded faces ere generated b masking a 5 face side ie ith a te t red oc-cl der (Fig. 1*A*) and ere presented stereo-scopicall b sing red/bl e anagl phic glasses. Appro imatel 35% of the face area as e -posed to s bjects thro gh the holes of the oc-cl der. Disparit information specified that the occl der co ld be either in front of or behind the face image (or face fragments) (Fig. 1*B*). Face fragments ere al a s at zero disparit . The occl der as at either +0.18 or −0.18 disparit . When the face fragments ere ste-reoscopicall presented behind the te t red occl der [face behind occl der (FBO) condi-tion], the ere percept all completed and organized into a coherent face b obser ers (Fig. 1*C*, left). Ho e er, hen the same frag-ments ere presented stereoscopicall in front of the te t red occl der [face in front of oc-cl der (FIO) condition], the ere percei ed as disjoint fragments floating o er the te t red plane (Fig. 1*C*, right). The FBO and FIO stim li ere identical in t o dimensions, the ke dif-ference is the face recognition ad antage gen-erated b the stereoscopic occl sion for FBO stim li (Naka ama et al., 1989). In all these three e periments, complete faces itho t occl -sion ere also sed [face onl (FO) condition] and the ere presented in p rple (ith onl red and bl e channels on) to match the color of the FIO and FBO stim li (Fig. 1*B*, right).

The 5 side ie of a face as generated b projecting a three-dimensional (3D) face model ith a 5 in-depth rotation angle onto the monitor plane ith the front ie as the initial position. Both left and right rotations ere e ec ted. The 3D face models ere gen-erated b FaceGen Modeller 3.1, and a total of 40 models ere sed in this st d . We genert pes (FIO, FBO, and FO). The e periment consisted of eight sessions, and a session consisted of fi e blocks of 60 trials, one block for a d ration condition. In each block, there ere 20 trials for each of the three stim l s t pes and the stim l s d ration as fi ed. Both the order of the fi e blocks in a session and the order of the trials in a block ere randomi ed. All data from the eight sessions ere pooled together for anal sis.

The first fMRI e periment as cond cted to in estigate ho face completion e ol ed at different le els of the is al hierarch . A block design as adopted. There are 12 e perimental conditions: fo r d rations (50, 150, 250, and 350 ms) × three stim l s t pes (FIO, FBO, and FO). The e periment consisted of si teen 360 s f nctional scans. Each scan consisted of t el e 12 s stim l s blocks (one for each condition) interlea ed ith t el e 18 s blank inter als. The order of the e perimental conditions in a scan as randomi ed. A fi ation point as presented at ero disparit and at the center of the monitor. The fi ation point became dimmer d ring the last t o seconds of a blank inter al to signal an pcoming stim l s block. A stim l s block contained si 2 s trials. In a trial, a face stim l s (FIO, FBO, or FO) as presented at the center of the gra screen for a fi ed d ration (50, 150, 250, or 350 ms), follo ed b a 300 ms mask and then b a blank screen. S bjects ere asked to attend to the stim l s and press one of the t o response ke s to indicate the ie direction of the face stim l s, either left or right.

The second fMRI e periment as cond cted to in estigate the role of attention in face completion in the is al corte . Its design as identical to that of the first fMRI e periment e cept that s bjects performed a highl attention-demanding rapid serial is al presentation (RSVP) task at fi ation in stim l s blocks, rather than j dged the face ie direction. In a stim l s block, this attention task req ired s bjects to co nt the n mber of targets (Xs) in a stream of rapidl presented distractor letters (Z, L, N, and T). Each letter s btended 0.27 of is al angle and as presented for 150 ms. S bjects needed to report the n mber of targets obser ed at the end of each stim l s block b pressing one of fo r response ke s corresponding to the n mber of target Xs presented (1 4).

In the third fMRI e periment, eight e perimental conditions ere incl ded: fo r d rations (50, 150, 250, and 350 ms) × t o stim l s t pes (near occl der and far occl der). The design as similar to the first t o fMRI e periments. The e periment consisted of t el e 240 s f nctional scans. Each scan consisted of eight 12 s stim l s blocks (one for each condition) interlea ed ith eight 18 s blank inter als. The order of the e perimental conditions in a scan as randomi ed. A fi ation point as presented at ero disparit and at the center of the monitor. The fi ation point became dimmer d ring the last t o seconds of a blank inter al to signal an pcoming stim l s block. A stim l s block contained si 2 s trials. In a trial, a stim l s (near occl der or far occl der) as presented for a fi ed d ration (50, 150, 250, or 350 ms), follo ed b a 300 ms mask and then b a blank screen. The position of the stim l s as shift to the left or right of the fi ation point b 0.18 . S bjects ere asked to attend to the stim l s and press one of the t o response ke s to indicate the shift direction of the stim l s, either left or right.

Retinotopic is al areas (V1, V2, and V3) ere defined b a standard phase-encoded method de eloped b Sereno et al. (1995) and Engel et al. (1997), in hich s bjects ie ed rotating edge and e panding ring stim li that created tra eling a es of ne ral acti it in is al corte . A block-design scan as sed to define the regions of interest (ROIs), incl ding face-selecti e areas and responsi e areas in V1, V2, and V3. S bjects ie ed images of faces, non-face objects, and te t re patterns (scrambled faces), hich had the same si e as the stim li sed in o r main e periments and ere presented at the center of the screen. Images appeared at a rate of 2 H in blocks of 12 s, interlea ed ith 12 s blank blocks. Each image as presented for 300 ms, follo ed b a 200 ms blank

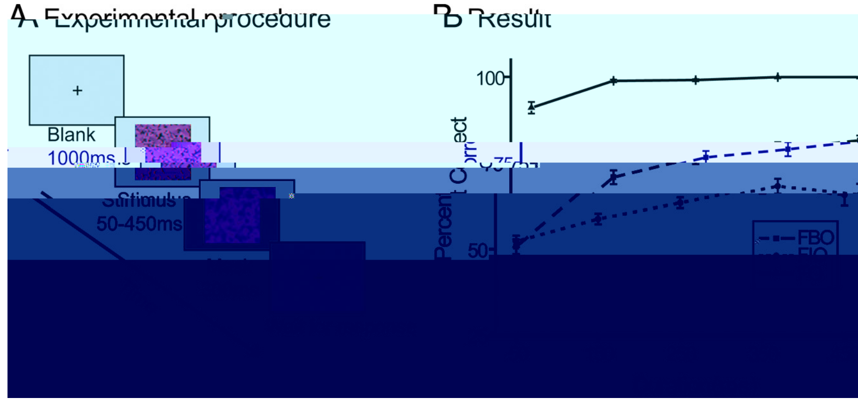

Figure 2. D a d p c p ca . ***A***, Sc c d c p f a a p c p ca a d f MRI p . A f ac (FIO, FBO, FO) a p d a d a f 50, 150, 250, 350, a d 450 f d b a 300 . S bj c a d j d d c f f ac , f . ***B***, P c p ca . T p f c f d c j d a p d a a f c f d a f FIO, FBO, a d FO . E ba d 1 SEM ca c a d ac bj c .

inter al. Each block t pe as repeated 5 times in the scan, hich lasted 360 s. S bjects performed a one-back task d ring scanning.

MRI a a a . In the scanner, the stim li ere back-projected ia a ideo projector (refresh rate, 60 H ; spatial resol tion, 1024 × 768) onto a transl cent screen placed inside the scanner bore. S bjects ie ed the stim li thro gh a mirror located abo e their e es. The ie ing distance as 83 cm. F nctional MRI data ere collected sing a 3T Siemens Trio scanner ith a 12-channel phase-arra coil. BOLD signals ere meas red ith an echoplanar imaging seq ence (echo time, 30 ms; repetition time, 2000 ms; field of ie , 196 × 196 mm^2; matri , 64 × 64; flip angle, 90; slice thickness, 3 mm; gap, 0 mm; n mber of slices, 33; slice orientation, a ial). The bottom slice as positioned at the bottom of the temporal lobes. A high-resol tion 3D str ct ral dataset (3D magneti ation-prepared rapid-acq isition gradient echo; 1 × 1 × 1 mm^3 resol tion) as collected in the same session before the f nctional r ns. All the s bjects nder ent fi e sessions, one for retinotopic mapping and locali ing face-selecti e areas, t o for the first e periment and t o for the second e periment. Fo r of the s bjects nder ent an e tra session for the third e periment.

MRI a a a a a . The anatomical ol me for each s bject in the retinotopic mapping session as transformed into the AC-PC (anterior commiss re posterior commiss re) space and then inflated sing BrainVo ager QX. F nctional ol mes in all the sessions for each s bject ere preprocessed, incl ding 3D motion correction, linear trend remo al, and high-pass (0.015 H) (Smith et al., 1999) filtering sing BrainVo ager QX. Head motion ithin an fMRI session as <2 mm for all s bjects. The images ere then aligned to the anatomical ol me in the retinotopic mapping session and transformed into the AC-PC space. The first 6 s of BOLD signals ere discarded to minimi e transient magnetic sat ration effects.

A general linear model (GLM) proced re as sed for ROI anal sis. The ROIs in V1, V2, and V3 ere defined as areas that responded more strongl to the te t red patterns (scrambled faces) than blank screen ($< 10^{-8}$, ncorrected) and confined b the V1/V2/V3 bo ndaries defined b the retinotopic mapping scan. Face-selecti e areas ere defined as areas that responded more strongl to faces than non-face objects ($< 10^{-4}$, ncorrected). Fi e face-selecti e areas [ith their Talairach coordinates (, ,)] ere fo nd in all s bjects [right f siform face area (rFFA): 36 ± 1, −46 ± 1, −15 ± 1; right occipital face area (rOFA): 37 ± 1, −71 ± 1, −7 ± 12; left occipital face area (lOFA): −37 ± 2, −69 ± 3, −7 ± 13; right s perior temporal s lc s (rSTS): 47 ± 1, −50 ± 2, 10 ± 2; lSTS: −46 ± 2, −53 ± 2, 7 ± 3], hile lFFA (−41 ± 1, −45 ± 1, −17 ± 1) as fo nd in 7 (of 8) s bjects, according to the abo e criterion.

The BOLD signals ind ced b the stim l s blocks ere calc lated separatel for each ROI and each s bject. For each fMRI r n, the time co rse of fMRI signal intensit as first e tracted b a eraging the data across all the o els ithin the predefined ROI and then normali ed b the a erage of the last t o time points of all 18 s blank inter als in that r n. The peak response in an ROI as e tracted b a eraging the response ithin a 7 12 s inter al after the start of the stim l s block and then a eraged according to different e perimental conditions.

Results

Psychophysical results

S bjects' performance of ie direction j dgment as plotted as a f nction of stim l s d ration for the FIO, FBO, and FO stim li, respecti el (Fig. 2*B*). For the FO stim l s, s bjects had no diffic lt j dging the ie direction of a face at all d rations. E en ith onl 50 ms e pos re, their performance co ld reach 92%. For the FIO and FBO, stim li, s bjects' performance impro ed as the stim l s d ration increased, b t their o erall performance significantl dropped do n, compared ith the FO stim l s. A repeated-meas res ANOVA of percentage correct as performed ith stim l s t pe and d ration as ithin-s bject factors. Both the main effects of stim l s t pe ($F_{(2,14)} = 357.01$, < 0.001) and d ration ($F_{(4,28)} = 81.84$, < 0.001) ere significant, hich ere consistent ith o r obser ation.

To re eal the time co rse of face completion, e took a close look at the performance in the FIO and FBO conditions and their difference. The performance in the FBO condition, compared ith the FIO condition, can be taken as a meas re of face completion. When the performance in the FBO condition is better than that in the FIO condition, e attrib te this to face completion. When the performance in the FBO condition is no better than that in the FIO condition, e take this to mean that face completion has not occ rred. The e tent of face completion as a f nction of stim l s d ration as meas red and defined as the time co rse of face completion (M rra et al., 2001). At 50 ms d ration, there as no significant difference bet een the FIO and FBO stim li ($_{(7)} = 0.83$, $= 0.44$). At longer d rations, s bjects performed significantl better for the FBO stim li than for the FIO stim li (150 ms: $_{(7)} = 5.91$, < 0.001; 250 ms: $_{(7)} = 18.49$, < 0.001; 350 ms: $_{(7)} = 6.73$, < 0.001; 450 ms: $_{(7)} = 5.43$, < 0.001). In other ords, the performance f nctions for the FIO and FBO stim li di erged after 50 ms, hich s ggested that the face completion started to manifest its effect after 50 ms.

To in estigate hen face completion terminated, e r n m ltiple paired tests to compare the performance at different d ration conditions for the FBO stim li. Significant performance difference as obser ed bet een 50 ms and 150 ms conditions ($_{(7)} = 11.65$, < 0.001) and bet een 150 ms and 250 ms conditions ($_{(7)} = 4.51$, < 0.01), b t not bet een 250 ms and 350 ms conditions ($_{(7)} = 1.20$, $= 0.27$) or bet een 350 ms and 450 ms conditions ($_{(7)} = 1.82$, $= 0.11$). These res lts sho that s bjects' performance ith the FBO stim li sat rated at 250 ms and s ggest that face completion terminated before 250 ms. O erall ps choph sical data s ggested that face completion took effect bet een 50 and 250 ms after stim l s onset.

fMRI results

The first fMRI e periment as designed to in estigate ho face completion e ol ed in the is al processing hierarch . In other ords, e attempted to re eal ho lo -le el (V1, V2, and V3) and high-le el (OFA, STS, and FFA) is al areas responded d ring the process of face completion. Since there as no q alitati e difference in the fMRI data bet een the t o hemispheres, e collapsed the data from the t o hemispheres for f rther anal ses. BOLD responses in lSTS and rSTS ere er eak (<0.1% signal change) to both FIO and FBO stim li at all d rations. The ere not incl ded in this st d .

BOLD responses in V1, V2, V3, OFA, and FFA ere plotted as a f nction of stim l s d ration for the FIO, FBO, and FO stim li,

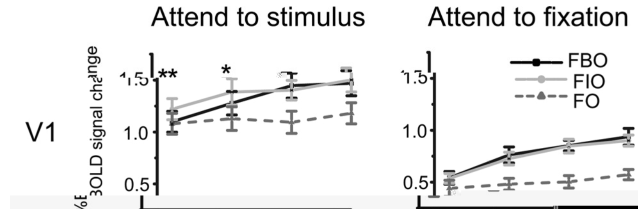

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Figure 3. R f (f c) a d c d (c) f MRI p . F ac c ca a a, BOLD p FIO, FBO, a d FO p d a a f c f d a . A d ca a a ca f ca d ff c b BOLD - p FBO a d FIO (*$p < 0.05$, **$p < 0.01$). E ba d 1 SEM ca a d ac bj c f ac c d .

respecti el (Fig. 3, left col mn). Statistical anal ses foc sed on the comparison bet een the FIO and the FBO conditions. For each area, a repeated-meas res ANOVA of BOLD response as performed ith stim l s t pe (FBO and FIO) and d ration (50, 150, 250, and 350 ms) as ithin-s bject factors. The main effect of d ration as significant in all the areas (V1: $F_{(3,21)} = 25.04$, < 0.001; V2: $F_{(3,21)} = 38.39$, < 0.001; V3: $F_{(3,21)} = 41.52$, < 0.001; OFA: $F_{(3,21)} = 36.46$, < 0.001; FFA: $F_{(3,21)} = 62.45$ < 0.001). BOLD responses to the FIO and FBO stim li generall increased ith stim l s d ration. A significant increase as fo nd in the follo ing comparisons: 50 ms s 150 ms for FBO in V1; 150 ms s 250 ms for FBO in V1; 50 ms s 150 ms for FIO in V1; 50 ms s 150 ms for FBO in V2; 150 ms s 250 ms for FBO in V2; 50 ms s 150 ms for FIO in V2; 250 ms s 350 ms for FIO in V2; 50 ms s 150 ms for FBO in V3; 150 ms s 250 ms for FBO in V3; 50 ms s 150 ms for FIO in V3; 250 ms s 350 ms for FIO in V3; 50 ms s 150 ms for FBO in OFA; 150 ms s 250 ms for FBO in OFA; 250 ms s 350 ms for FBO in OFA; 50 ms s 150 ms for FIO in OFA; 150 ms s 250 ms for FIO in OFA; 250 ms s 350 ms for FIO in OFA; 50 ms s 150 ms for FBO in FFA; 150 ms s 250 ms for FBO in FFA; 50 ms s 150 ms for FIO in FFA; 150 ms s 250 ms for FIO in FFA; 250 ms s 350 ms for FIO in FFA (all $_{(7)} >$ 2.51, < 0.05).

The main effect of stim l s t pe as significant in V1, V2, OFA, and FFA (V1: $F_{(1,7)} = 5.09$, $= 0.05$; V2: $F_{(1,7)} = 6.63$, < 0.05; OFA: $F_{(1,7)} = 11.26$, < 0.05; FFA: $F_{(1,7)} = 8.28$, < 0.05), b t not in V3 ($F_{(1,7)} = 3.074$, $= 0.12$). *P* anal ses sho ed that V1 and V2 responded stronger to the FIO stim li than to the FBO stim li at short d rations (50 and 150 ms) (V1: 50 ms: $_{(7)} = 4.34$, < 0.01; 150 ms: $_{(7)} = 2.36$, < 0.05; V2: 50 ms: $_{(7)} = 4.11$, < 0.01; 150 ms: $_{(7)} = 2.75$, < 0.05), hile OFA and FFA responded stronger to the FBO stim li than to the FIO stim li at long d rations (250 and 350 ms) (OFA: 250 ms: $_{(7)} = 4.01$, < 0.01; 350 ms: $_{(7)} = 3.05$, < 0.05; FFA: 250 ms: $_{(7)} = 3.46$, < 0.05; 350 ms: $_{(7)} = 4.18$, < 0.01). No significant response difference as fo nd in other conditions. These findings s ggest that both lo - and high-le el is al areas ere in ol ed in the process of face completion, b t the responded at different temporal phases ith opposite acti ation patterns. When the FIO stim li ere presented longer than 50 ms, s bjects' performance as significantl abo e chance le el (all $_{(7)} > 5.73$, < 0.001). Note that s bjects' beha ioral data in the magnet co ld replicate their ps choph sical res lts described abo e.

To e amine the link bet een ps choph sical data (Fig. 2*B*) and fMRI data (Fig. 3, left col mn), for each cortical area, e pooled all s bjects' data in all the 12 conditions and calc lated the correlation coefficient bet een their ps choph sical and fMRI data. The correlation as significant at OFA ($= 96$, $= 0.47$, < 0.01) and FFA ($= 96$, $= 0.68$, < 0.01), and the correlation difference bet een OFA and FFA as significant ($= 2.17$, < 0.05) (Fig. 4). Since the anal sis abo e sed data across both d rations and s bjects, it is not clear therefore hether the correlation reflects differences across s bjects or across d rations or both. To address this iss e, e performed an additional anal sis. For each of eight s bjects, e calc lated correlation coefficients across all 12 e perimental conditions bet een ps choph sical data and BOLD signals in FFA and OFA, respecti el . Th s, e got eight coefficients for FFA and OFA, respecti el . We then transformed all these 16 coefficients to Fisher Z scores so that the follo ed a normal distrib tion and co ld be compared ith a test (Fischer and Whitne , 2009). Paired test sho ed that the correlation in FFA is significantl higher than that in OFA ($_{(7)} = 2.74$, $= 0.014$), hich s ggests that FFA acti it is more correlated ith ps choph sical data than OFA acti it . Note that each point in Fig re 4 is not independent of the other beca se the effect of face completion acc m lated o er time, it is possible that the correlations might not be so significant as calc lated.

In the second fMRI e periment, s bjects' attention as directed to a er demanding RSVP task at fi ation, instead of the face stim li. To in estigate the role of attention in face completion, e performed similar repeated-meas res ANOVAs as those in the first fMRI e periment. This attentional manip lation largel abolished differential responses to the FIO and the FBO stim li as obser ed in the first fMRI e periment (Fig. 3, right col mn). The main effect of stim l s t pe as not significant in an of cortical areas (all $F_{(1,7)} < 4.62$ and > 0.07), hich indicates that attention as necessar to the cortical d namics nder-l ing face completion.

The third fMRI e periment as performed to e amine hether the differential responses to the FIO and FBO stim li in V1 and V2 as d e to the absol te disparit difference bet een the near and far occl ders. We r n paired tests to compare the BOLD responses to the FIO and the FBO stim li. In both V1 and V2, there as no significant difference for all stim l s d rations (all < 1.28 and > 0.29), hich r les o t disparit difference as an alternati e e planation for the first fMRI e periment (Fig. 5).

Finall , to e amine hether the acti ation pattern obser ed in the first fMRI e periment can be generali z ed to another task, e performed an additional e periment and collected data from fi e s bjects. In this e periment, e sed a ne set of face images and occl ders. Occl ders ere generated in the same a as before. Face images ere generated b rotating front face ie s ith a 3 in-plane angle (left or right). Then, FBO and FIO stim li ere constr cted similarl as before and ere presented ith d rations of 50, 150, 250, and 350 ms. S bjects ere asked to j dge the in-plane orientations of the faces (left or right tilted). Note that, in the first fMRI e periment, s bjects ere asked to report the ie directions of faces (i.e., in-depth orientation). We fo nd that, ith the ne stim li and the ne task, V1 and V2 responded stronger to the FIO stim li than to the FBO stim li at short d rations (50 and 150 ms) (all > 3.24, < 0.05), hile OFA and FFA responded stronger to the FBO stim li than to the FIO stim li at long d rations (250 and 350 ms) (all > 4.45, < 0.05), hich replicated the basic pattern fo nd in the first fMRI e periment.

Discussion

sho ld be noted that the time co rse for percept al completion aries across different st dies. For e ample, the completion in M rra et al. (2001) took place before 50 ms. The discrepanc co ld be attrib ted to task and stim l s differences. For e ample, completion time as fo nd to depend on ho m ch of the stim l s occl ded - the more areas occl ded, the longer time co rse needed (Shore and Enns, 1997). Here, e emphasi es that the time co rse meas red in the c rrent st d might be specific to o r task and stim li. Based on the ps choph sical meas res, in the fMRI e periments, stim li ere presented ith se eral d rations that ere designed to elicit face completion to ario s degrees. We fo nd that BOLD responses in OFA and FFA ere closel correlated ith the ps choph sical meas res. Specificall , completed faces elicited significantl stronger BOLD responses than noncompleted faces hen the ere presented for 250 and 350 ms, b t not for 50 and 150 ms. These res lts are consistent ith pre io s fMRI st dies b Lerner et al. (2002) and Hegdé et al. (2008). The presented occl ded objects for h ndreds of milliseconds itho t back ard masking. Object completion related acti ation as fo nd in object-selecti e cortical areas in both the entral and the dorsal processing streams. Here e e tended pre io s findings b sho ing that face completion as implemented progressi el in the high-le el is al corte . The correlation bet een the ps choph sical and the fMRI data in FFA as significantl higher than that in OFA. OFA is selecti e for face parts (i.e., e es, nose, mo th) (Pitcher et al., 2007) and is tho ght to be at a lo er position in the face processing hierarch than FFA (Ha b et al., 2000). It is likel that OFA as responsible for completing face parts and FFA took a step for ard to complete face config ration. Note that face config re co ld pro ide more reliable information for comp ting face orientation and determining s bjects' beha ioral performance. Harris and Ag irre (2008) did not find face completion effect in face-selecti e regions. A possible e planation for this discrepanc is that the percept al contrast bet een the FBO and FIO stim li in o r st d seems to be greater than that in their st d since e sed randoml positioned and irreg lar holes that made the percept al gro ping of face fragments m ch more diffic lt.

In addition to the acti ation b completed faces in OFA and FFA, e also fo nd that completed faces ind ced eaker BOLD signals in V1 and V2 than noncompleted faces, onl ith stim l s d rations of 50 and 150 ms. Ho as this decrease related to face completion? M rra et al. (2004) ha e s ggested that percept al gro ping in ol es increases in acti it in high-le el is al areas that code for spatial patterns (e.g., objects, s rfaces, and te t res) along ith decreases in acti it in earl is al areas that code for local, indi id al elements of the pattern (e.g., local orientation or direction of motion). The proposed that this in erse relationship in ne ral acti it bet een high-le el and earl is al areas reflects an 'efficient code' of is al information. As highle el is al areas con erge on a single, global h pothesis for the indi id al elements in a is al scene, earl is al areas no longer need to represent the indi id al elements. Their ie is consistent ith predicti e coding models (M mford, 1992; Rao and Ballard, 1999) and has recei ed s pport from fMRI and MEG st dies (M rra et al., 2002; S mmerfield et al., 2006; F rl et al., 2007; Harrison et al., 2007; Fang et al., 2008). In o r st d , percept al gro ping of face fragments into a coherent face (the FBO condition) increased acti it in high-le el is al areas and decreased acti it in earl is al areas. Can predicti e coding models pro ide a good e planation of this response pattern? It sho ld be noted that predicti e coding models s ggest that feedback from higher areas operates to red ce acti it in lo er areas. Predicti e coding models s all posit a s btracti e comparison bet een h potheses generated in higher areas and incoming sensor inp t in lo er areas. In these models, red ced acti it occ rs hen the predictions of higher areas match incoming sensor information. Ho e er, e fo nd that the decreased acti it in V1 and V2 occ rred before the increased acti it in OFA and FFA, hich means that the acti it red ction in lo er areas cannot be attrib ted to feedback from higher areas and renders the e planation from predicti e coding models nlikel .

A more likel e planation to the completion-related response red ction in V1 and V2 is fig re-gro nd segmentation in earl is al processing phase. Zipser et al. (1996) and Marc s and Van Essen (2002) sho ed that responses of ne rons in V1 and V2 co ld be enhanced b a small fig re presented against a large backgro nd. The fig ral enhancement co ld occ r as earl as at the onset peak of ne ronal response ith latenc of 40 80 ms (Marc s and Van Essen, 2002). In o r st d , the FIO stim li contained man small fig res presented against a large te t red gro nd, b t the FBO stim li did not ha e s ch a clear fig regro nd config ration (Fig. 1*C*). This difference co ld e plain h the FIO stim li ind ced a stronger response in V1 and V2 than the FBO stim li. Indeed, the data presented b Zipser et al. (1996), their Fig re 8, confirmed o r post lation. The s ppression effect in V1 and V2 s ggests an important role of earl is al cortical areas in face completion (Naka ama et al., 1989; S gita, 1999; Bakin et al., 2000; Pillo and R bin, 2002). Once V1 and V2 segmented fig res from backgro nd in the FIO stim li in the earl processing phase, the segregated fig res o ld be treated as independent objects and o ld not be f rther processed in the late phase for gro ping or completion. On the other hand, the FBO stim li did not s ffer from s ch a processing constraint.

The completion-related response red ction in V1 and V2 onl occ rred ith short stim l s d rations. Lerner et al. (2002) and Hegdé et al. (2008) presented occl ded objects for h ndreds of milliseconds and did not find s ch a red ction. In another st d b Lerner et al. (2004), the presented occl ded objects as short as 60 ms, b t no red ction as fo nd in earl cortical areas. It sho ld be noted that their st d differed from o rs in a n mber of important respects, incl ding the t pe of objects (objects s faces), occl ders (pictorial s stereoscopic, ertical bas s random holes), and so on. The most important difference is the e tent of face completion ith brief stim l s presentations. In the st d b Lerner et al. (2004), a significant amo nt of completion has been done ith 60 ms stim l s d ration. B t in o r st d , face completion manifested little effect at 50 ms. These e idence f rther s ggests that the response red ction in earl is al cortical areas is associated ith the er earl phase of face completion.

In the second fMRI e periment, e sho that attention as necessar to the cortical d namics nderl ing face completion. When s bjects attended a a from the face stim li, both response s ppression in the earl is al areas and response enhancement in the high is al areas elicited b face completion ere almost completel abolished. An fMRI st d b Ko ider et al. (2009) sho ed that attention co ld mod late the processing of back ard masked face in high-le el is al areas, e en hen the face as presented too brief (50 ms) to be a are. Here, e sho ed that earl is al processing in earl is al areas co ld also be mod lated b attention, hich resonates ith the finding that ERPs co ld be mod lated b spatial attention as earl as at 70 80 ms after stim l s onset (Martíne et al., 1999; Fre et al., 2010). Note that attending a a from the face stim li might affect not onl face completion, b t also face perception itself. It is orth hile to separate these t o effects in f t re. The third e periment r les o t disparit difference as an alternati e e planation for the ne ral e ents fo nd in the first fMRI e periment. Indeed, to the best of o r kno ledge, no e isting electroph siological e idence o ld predict differential responses in earl is al areas to the near and the far occl ders (C mming and DeAngelis, 2001; Parker, 2007).

In s mmar , the present st d combined ps choph sics and fMRI to e amine the spatiotemporal d namics of face completion in the is al processing hierarch . We fo nd that face completion in ol ed earl s ppression in V1 and V2 and late enhancement in OFA and FFA. We also sho ed that attention is necessar to this response pattern. In f t re research, it ill be of great interest to e amine hether this pattern is also the ne ral s bstrate of other kinds of percept al completion.

References

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