SCIENTIFIC REPORTS

OPEN

Selective Audiovisual Semantic Integration Enabled by Feature-Selective Attention

Received: 28 May 2015
Accepted: 30 November 2015
Published: 13 January 2016

Yuanqing Li , Jinyi Long , Biao Huang , Tianyou Yu , Wei Wu , Peijun Li , Fang Fang & Pei Sun

An audiovisual object may contain multiple semantic features, such as the gender and emotional features of the speaker. Feature-selective attention and audiovisual semantic integration are two brain functions involved in the recognition of audiovisual objects. Humans often selectively attend to one or several features while ignoring the other features of an audiovisual object. Meanwhile, the human brain integrates semantic information from the visual and auditory modalities. However, how these two brain functions correlate with each other remains to be elucidated. In this functional magnetic resonance imaging (fMRI) study, we explored the neural mechanism by which feature-selective attention modulates audiovisual semantic integration. During the fMRI experiment, the subjects were presented with visual-only, auditory-only, or audiovisual dynamical facial stimuli and performed several feature-selective attention tasks. Our results revealed that a distribution of areas, including heteromodal areas and brain areas encoding attended features, may be involved in audiovisual semantic integration. Through feature-selective attention, the human brain may selectively integrate audiovisual semantic information from attended features by enhancing functional connectivity and thus regulating

An a dio i al objec in he eal o ld ma con ain m l iple eman ic fea e , ch a he gende and emo ional fea e of a peake face and oice. D ing he ecogni ion of an a dio i al objec , he h man b ain in eg a e he eman ic info ma ion f om he e fea e ob ained b he i al and he a di o modali ie , i.e., a dio i al eman ic in eg a ion ma occ in he b ain. A dio i al in eg a ion facili a e apid, ob and a oma ic objec pe cep ion and ecogni ion[1 3]. Compa i on of i al-onl and a di o -onl im li ha e e ealed ha cong en a dio i al im li lead o onge ne al e pon e han ei he pe of im l alone in he po e io

occ a di e en le el , ch a lo -le el a dio i al en o in eg a ion, in hich he eman ic info ma ion of he a dio i al im li i no in ol ed, and high-le el a dio i al eman ic in eg a ion[10], die of a dio i al eman ic in eg a ion ha e been limi ed compa ed i h die of a dio i al en o in eg a ion. In pa ic la , he mechani m nde l ing he mod la ion of a dio i al eman ic in eg a ion in he b ain b fea e- elec i e a en ion ha e no been el cida ed.

P e io die ha e mainl foc ed on c o modal a en ion and e plo ed ho c o modal a en ion mod-la e a dio i al en o in eg a ion ac o a io age . Fo e ample, in a d of he in e ac ion be een m l i en o in eg a ion and a en ion ing non- eman ic i al-onl , a di o -onl and a dio i al im li[11], an anal i of e en - ela ed po en ial (ERP) indica ed ha he e ec of m l i en o in eg a ion eq i e ha he m l i en o objec be f ll a ended. e a dio i al en o in eg a ion of mo ion info ma ion in ol e

[1]Center for Brain Computer Interfaces and Brain Information Processing, South China University of Technology, Guangzhou, 510640, China. [2]Department of Radiology, Guangdong General Hospital, Guangzhou, 510080, China. [3]Department of Psychology and Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing 100871, China. [4]Department of Psychology, School of Social Sciences, Tsinghua University, Beijing, 100084, China. [5]Guangzhou Key Laboratory of Brain Computer Interaction and Applications, Guangzhou 510640, China. Correspondence and requests for materials should be addressed to Y.L. (email: auyqli@scut.edu.cn)

a peci c ne o k in hich he pa ie al and pe hap la e al f on al co ice appea o be op imall i a ed o media e he in eg a ion and a en ional elec ion of mo ion info ma ion ac o modali ie [12]. In a dio i al face pe cep ion, c o modal a en ion in ence c o modal binding d ing peech eading[13,14]. , a en ion and a dio i al in eg a ion in e ac i h each o he in a ophi ica ed manne . Ho e e , fea e- elec i e a en ion in a dio i al condi ion and he ela ion hip be een fea e- elec i e a en ion and high-le el a dio i al eman ic in eg a ion emain o be e plo ed.

In a ingle (i al o a di o) modali , fea e- elec i e a en ion ma lead o elec i e p oce ing of he a ended fea e of an objec in he b ain[7 9,15 17]. Nob e *et al.*[8] demon a ed ha ERP a e mod la ed b fea e- elec i e a en ion and ha i ele an fea e a e inhibi ed d ing he ea l age of pe cep al anal i in h man . In monke , Mi abella *et al.*[17] ob e ed ha ne on in i al a ea V4 e hibi elec i i o elemen al objec fea e . Ba ed on he e die ha ha e emplo ed nimodal im li, he e e e plo e he he and ho a imila fea e- elec i e a en ion mechani m in an a dio i al condi ion i in ol ed in a dio i al eman ic in eg a ion.

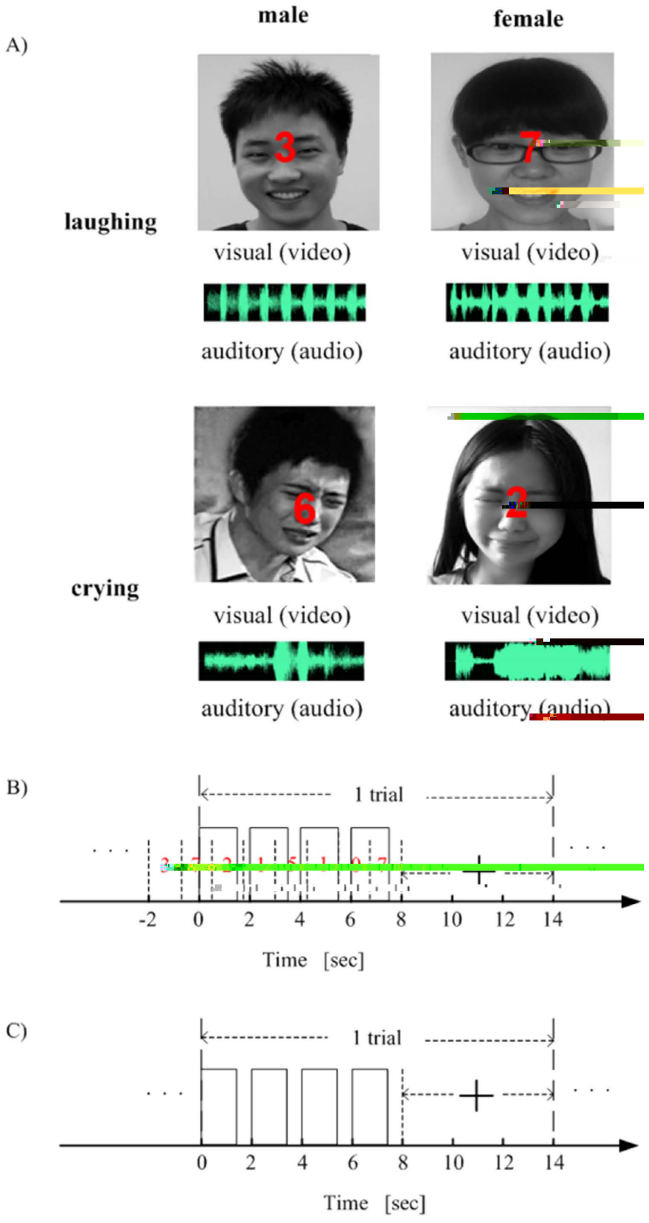

Figure 1. Experimental stimuli and time courses. (**A**) Fo e ample of a dio i al im li; he ed n mbe indica e n i h he n mbe a k onl . (**B**) Time co e of a ial fo he n i h he n mbe a k, in hich he im li incl ded andoml p e en ed n mbe and ideo /a dio /mo ie clip . (**C**) Time co e of a ial fo he n i h he gende , emo ion, o bi-fea e a k. Fo bo h (**B**,**C**), he p e en a ion of a im l (ideo/ a dio/mo ie clip) la ed 1,400 m and a epea ed fo ime d ing he eigh econd in a ial. A i al c e (+) appea ed a he 8 h econd and pe i ed fo i econd .

Fo each of he h ee n i h he n mbe a k, in addi ion o he co e ponding a dio i al, i al-onl , o a di o -onl facial im li f om he mo ie clip , n mbe in ed appea ed eq en iall a he cen e of he c een (ee Fig. 1A). e bjec ' a k a o a end o he n mbe in ead of he o he im li (ee Table 1). We de igned a di c l n mbe a k fo he bjec in hich he e e a ked o nd and co n he epea ed n mbe o en e ha he f ll igno ed he fea e of he i al-onl , a di o -onl , o a dio i al facial im li. e efo e, he bjec pe fo med hi a k i h lo acc ac , a ho n in Fig. S3. A he beginning of each block, he e e e fo econd befo e he ial, and a ho in c ion in Chine e (ee Table 1) a di pla ed on he c een in he o econd (he la o econd e e ed o di pla n mbe , a indica ed belo). A he beginning of each ial, a i al-onl , a di o -onl o a dio i al facial im l a p e en ed o he bjec fo 1,400 m , follo ed b a 600-m blank pe iod. i o- econd c cle i h he ame im l a epea ed fo ime , follo ed b a i - econd blank pe iod. e efo e, one ial la ed 14 econd . In addi ion o he abo e im li, eigh n mbe in ed appea ed one b one a he cen e of he c een, each a andom in ege f om 0 o 9. Each n mbe la ed 900 m , and he in e al be een o b eq en n mbe a 350 m . e n mbe appea ed 2 econd befo e he beginning of hi ial. e bjec e e a ked o nd and co n he epea ed n mbe . A e he im la ion, a

a ion c o appea ed on he c een. e bjec hen e ponded b p e ing he igh -hand ke acco ding o he in c ion fo hi block (ee Table 1). e a ion c o changed colo a he 12 h econd, indica ing ha he ne ial o ld begin ho l (ee Fig. 1B). In o al, a n la ed 1,350 econd .

e p oced e fo he h ee n i h he gende /emo ion a k a imila o ha fo he n i h he n mbe a k, e cep ha no n mbe appea ed on he c een and he bjec pe fo med a gende /emo ion j dgmen a k (See Table 1). Speci call , he bjec e e a ked o foc hei a en ion on ei he he gende o he emo ion of he29(o)15 h (i n)9 -3.1icii n le(ci c)(l-( )-5.1(5c)-3.1(75.2(l)6.9()3.8(ei d)11.8(n e68(n f)8.84(e-5.--8(e)-5c)-3.1(5)-5.1(2

o el , ime e ie de ending, and no mali a ion of he ime e ie in each block o e o mean and ni a i-ance. All p ep oce ing ep e e pe fo med ing SPM8[23] and c om f nc ion in MATLAB 7.4 (Ma hWo k , Na ick, Ma ach e , USA).

Univariate GLM analysis. i e pe imen incl ded fo e pe imen al a k (n mbe , gende , emo ion, and bi-fea e). Fo each e pe imen al a k, h ee n co e ponding o he i al-onl , he a di o -onl , and he a dio i al im l condi ion e e pe fo med. To con m ha a dio i al en o in eg a ion occ ed fo each e pe imen al a k and de e mine he he e omodal a ea a ocia ed i h a dio i al in eg a ion, e pe fo med o el- i e g o p anal i of he fMRI da a ba ed on a mi ed-e ec o-le el GLM in SPM8. In pa ic la , ing he da a f om he h ee n mbe n , e pe fo med GLM anal i o e plo e he a dio i al in e-g a ion a he en o le el hen he bjec f ll igno ed he i al-onl , a di o -onl , o a dio i al facial im li hile onl a ending o he n mbe . e GLM anal i incl ded he follo ing da a p oce ing. e fMRI da a fo each bjec e e bjec ed o a -le el GLM, and he e ima ed be a coe cien ac o all bjec e e hen combined and anal ed ing a econd-le el GLM. e follo ing a i ical c i e ion a ed o de e mine b ain a ea fo a dio i al en o in eg a ion: [AV>ma (A,V) ($p < 0.05$, FWE-co ec ed)] ∩ [V>0 o A>0 ($p < 0.05$, nco ec ed)][1,4,6,24–27], he e ∩ deno e he in e ec ion of o e . Fo each bjec , each a k, and each im l condi ion, e al o comp ed he pe cen ignal change of he pSTS/MTG cl e ia egion-of-in e e (ROI)-ba ed anal i (implemen ed b he MATLAB oolbo Ma BaR-0.43[28]). Speci call , e iden i ed he cl e con i ing of igni can l ac i a ed o el in he bila e al pSTS/MTG ia g o p GLM anal i a abo e. Fi , a GLM model a e ima ed f om he mean BOLD ignal of he cl e , and he pe-cen ignal change in he cl e a hen comp ed a he a io be een he ma im m of he e ima ed e en e pon e and he ba eline.

MVPA procedure for the calculation of the reproducibility ratio and decoding accuracy. Fo each bjec , he e e e a o al of 12 n i h fo e pe imen al a k and h ee im l condi ion . Fo each n, e calc la ed a ep od cibili a io co e ponding o he gende fea e and one co e ponding o he emo-ion fea e b appl ing an MVPA me hod o he fMRI da a. e ep od cibili a io i an inde ha mea e he imila i of he ne al ac i i pa e n i hin a cla (e.g., he male cla in he gende dimen ion) and he di e ence in ne al ac i i pa e n be een o cla e (e.g., male . female in he gende dimen ion). e highe he ep od cibili a io, he onge he imila i of b ain pa e n i hin each cla and he la ge he di e ence be een he o cla e of b ain pa e n a ocia ed i h he o gende o o emo ion ca ego ie . U ing he fMRI da a, e al o decoded he gende and emo ion ca ego ie of he im li pe cei ed b he bjec . e ne al ep e en a ion of gende and emo ion fea e e e anal ed b compa ing he ep od cibili a io o decoding acc ac a e fo di e en im l condi ion (i al-onl , a di o -onl , and a dio i al) and e pe imen al a k (n mbe , gende , emo ion, and bi-fea e). In pa ic la , he bjec onl a ended o he n mbe d ing he h ee n mbe n , b he MVPA a ba ed on he gende and emo ion fea e of he i al-onl , a di o -onl , o a dio i al facial im li. In hi manne , e anal ed he ne al ep e en a ion of gende and emo ion fea e hen none a a ended. Belo , e e plain he MVPA p oced e fo gende ca ego ie (he MVPA p oced e fo emo ion ca ego ie a imila).

Fo each n, 10-fold c o - alida ion a pe fo med fo he calc la ion of he ep od cibili a io and decoding acc ac co e ponding o he o gende ca ego ie (efe o Fig. S1 in S pplemen al Info ma ion). Speci call , he da a f om 80 ial e e eq all pa i ioned in o 10 non-o e lapping da a e . Fo he k h fold of he c o - alida ion ($k = 1, \ldots, 10$), he k h da a e (eigh ial) a ed fo he e , and he o he nine da a e (72 ial) e e ed fo o el elec ion and cla i e aining. A e he 10-fold c o - alida ion, he a e age ep od cibili a io and decoding acc ac a e e e calc la ed ac o all fold . e da a p oce ing p oced e fo he k h fold incl ded he follo ing:

1) Voxel selection based on the training data. A phe ical ea chligh algo i hm ha a eq en iall cen e ed a each o el i h a 3-mm adi ea chligh highligh ing 19 o el a applied o he aining da a e fo o el elec ion[29]. Wi hin each ea chligh co e ponding o a o el, e comp ed a Fi he a io h o gh Fi he linea di c iminan anal i , and hi a io indica ed he le el of di c imina ion be een he o gende ca ego ie in he local neighbo hood of hi o el. A Fi he a io map a h ob ained fo he hole b ain. K info ma i e o el i h he highe Fi he a io e e hen elec ed (e.g., $K = 1500$ in hi d).

2) Pattern extraction. U ing he K elec ed o el , e con c ed a K-dimen ional pa e n ec o fo each ial of he aining da a in hich each elemen ep e en ed he mean BOLD e pon e of a elec ed o el f om he 6 h o he 14 h econd of hi ial (he la fo ol me , o acco n fo he dela in he hemod namic e pon e; each ial la ed 14 econd). S( )ia 9olJ/Tc J-0.0(e)-5-8(o)(a)73(a)3 ad a K-dim3en ional pa n ec ad a he he.9(n B)-( )-6(i)-2.9

he e $\theta_{i,j}$ i he angle be een o pa e n ec o P_i

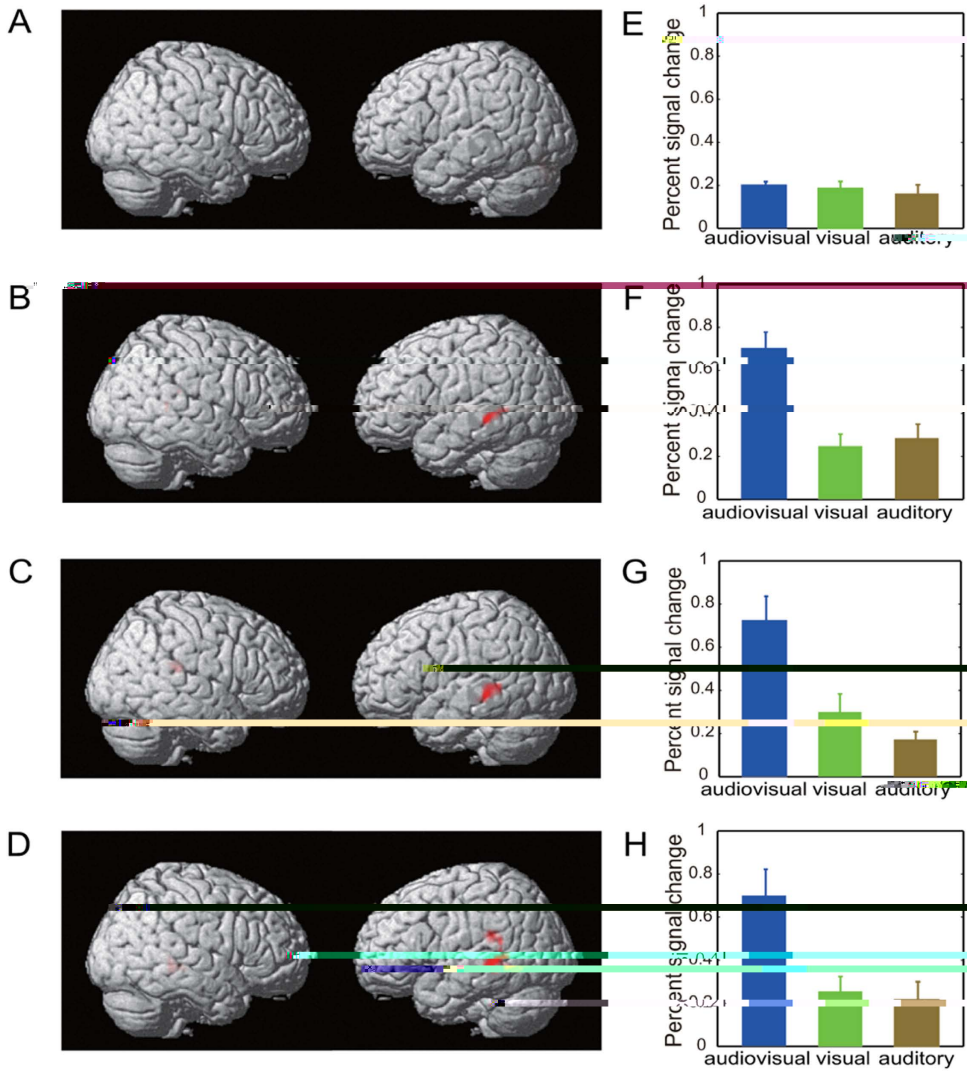

Figure 2. Brain areas for audiovisual sensory integration that met the criterion [AV>max (A,V) ($p < 0.05$, FWE-corrected)]∩[V>0 or A>0 ($p < 0.05$, uncorrected)]. (**A**) No b ain a ea e hibi ed a dio i al en o in eg a ion fo he n mbe a k. (**B**) B ain a ea e hibi ing a dio i al en o in eg a ion fo he gende a k, incl ding he le pSTS/MTG (Talai ach coo dina e of he cl e cen e : (−57, −34, −5); cl e i e: 76). (**C**) B ain a ea e hibi ing a dio i al en o in eg a ion fo he emo ion a k, incl ding he le pSTS/MTG (cl e cen e : (−60, −40, 1); cl e i e: 98) and he igh pSTS/MTG (cl e cen e : (45, −34, 19); cl e i e: 13). (**D**) B ain a ea e hibi ing a dio i al en o in eg a ion fo he bi-fea e a k, incl ding he le pSTS/MTG (cl e cen e : (−54, −

di e en ia ed fo di e en e pe imen al a k o di e en eman ic fea e . , a dio i al en o in eg a ion a he han a dio i al eman ic in eg a ion occ ed in he iden i ed he e omodal a ea of he pSTS/MTG, con i en i h p e io e l [10].

MVPA results of the reproducibility ratios and decoding accuracy rates. U ing an MVPA me hod, fo each of he 12 n of he e pe imen i h fo a en ional a k and h ee im l condi ion , e calc la ed o ep od cibili a io co e ponding o he gende ca ego ie (male . female) and he emo ion ca ego- ie (c ing . la ghing) of he im li e pec i el . F he mo e, each calc la ion of ep od cibili a io a ba ed on 1500 elec ed o el (ee Ma e ial and Me hod); he e l of ep od cibili a io a e, ho n in Fig. 3. We al o , ema icall a ied he n mbe of elec ed o el f om 25 o 1500 o calc la e he ep od cibili a io and ob ained imila e l (ee Fig. S4).

Fo he ep od cibili a io of he gende /emo ion ca ego ie , o- a epea ed mea e ANOVA e ealed igni can main e ec of im l condi ion (gende ca ego ie : $p < 10^{-17}$, $F(2, 8) = 88.73$; emo ion ca ego ie : $p < 10^{-16}$, $F(2, 8) = 51.37$) and e pe imen al a k (gende ca ego ie : $p < 10^{-17}$, $F(3, 8) = 81.13$; emo ion ca ego ie :

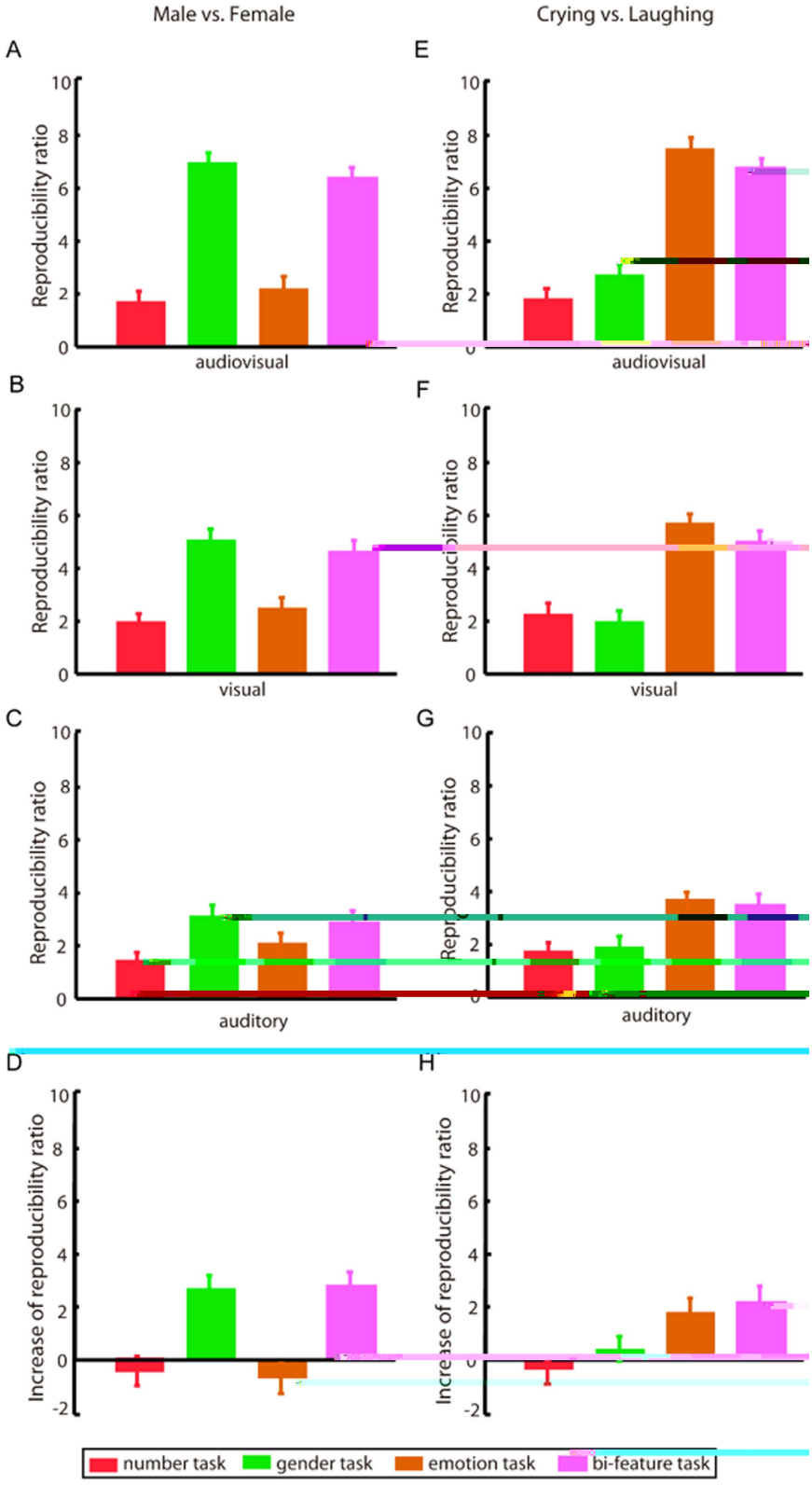

Figure 3. Reproducibility ratios (means and standard errors across all subjects) and the corresponding comparison results. Le /Righ : gende /emo ion ca ego ie ; he 3 o : a dio i al, i al-onl , and a di o -onl im l condi ion , e pec i el ; he 4 h o : he ep od cibili a io in he a dio i al condi ion min he ma im m of he ep od cibili a io in he i al-onl and a di o -onl condi ion .

$p < 10^{-17}$, $F(3, 8) = 68.26$) (Fig. 3A C,E G). e e a al o a igni can in e ac ion e ec be een he o fac o of im l condi ion and e pe imen al a k (gende ca ego ie : $p < 10^{-17}$, $F(6, 8) = 30.07$; emo ion ca ego ie : $p < 10^{-8}$, $F(6, 8) = 10.05$). Po hoc Bonfe oni-co ec ed pai ed - e on he im l condi ion e ealed he follo ing: (i) fo each a k- ele an fea e (gende ca ego ie i h he gende o he bi-fea e a k, le panel of Fig. 3; emo ion ca ego ie i h he emo ion o he bi-fea e a k, igh panel of Fig. 3), he ep od cibili a io e e igni can l highe fo he a dio i al im l condi ion han fo he i al- o a di o -onl im l condi ion (all $p < 0.001$ co ec ed); and (ii) fo each a k-i ele an fea e (gende ca ego ie i h he n mbe o he emo ion a k, le panel of Fig. 3; emo ion ca ego ie i h he n mbe o he gende a k, igh panel of Fig. 3), he e e e no igni can di e ence be een he a dio i al and he i al-onl o a di o -onl im l condi ion (all $p > 0.05$). F he mo e, po hoc Bonfe oni-co ec ed pai ed - e on he e pe imen al a k e ealed ha (i) in each of he a dio i al, i al-onl and a di o -onl im l condi ion , he ep od cibili a io fo gende /emo ion ca ego ie e e igni can l highe fo each ele an a k (gende ca ego ie : he gende o he bi-fea e a k, le panel of Fig. 3; emo ion ca ego ie : he emo ion o he bi-fea e a k, igh panel of Fig. 3) han fo each i ele an a k (gende ca ego ie : he n mbe o he emo ion a k, le panel of Fig. 3; emo ion ca ego ie : he n mbe o he gende a k, igh panel of Fig. 3) (all $p < 0.05$, co ec ed) and ha (ii) in each of he a dio i al, i al-onl and a di o -onl im l condi ion , he e e e no igni can di e ence in he ep od cibili a io fo gende /emo ion ca ego ie be een o ele an a k o be een o i ele an a k (all $p > 0.05$).

Fo each n of he e pe imen , e f he calc la ed he decoding acc acie of he gende ca ego ie (male . female) and he emo ion ca ego ie (c ing . la ghing) (ee Ma e ial and Me hod), hich a e p e en ed in Fig. S5. e decoding e l al o e eal he enhancemen e ec p od ced b he a dio i al im li onl fo a k- ele an fea e (ee Fig. S5).

When he b ain i ecei ing bo h a di o and i al ignal , mo e ep od cible ep e en a ion ma be p o d ced e en if no a dio i al in eg a ion occ . We h cond c ed a con ol e pe imen ha incl ded an incon g en a dio i al n fo he gende a k and one fo he emo ion a k. e e pe imen al p oced e fo each n a imila o ha of he cong en a dio i al n i h gende /emo ion a k of he main e pe imen e cep ha he a dio i al im li e e incong en in he gende o emo ion dimen ion. e e pe imen al e l demon a ed ha compa ed i h he i al-onl and a di o -onl im l condi ion , he incong en a dio i al im li did no enhance he ne al ep e en a ion of he a ended fea e (ee he con ol e pe imen in he S pplemen al Info ma ion fo de ail).

MVPA results for informative voxels, cross-reproducibility ratios, and functional connectivity.

B appl ing an MVPA me hod o he da a collec ed in he a dio i al condi ion i h bi-fea e a k, e ob ained he info ma i e o el fo gende /emo ion ca ego di c imina ion (ee Ma e ial and Me hod). e di ib - ion of he e info ma i e o el a e p e en ed in Table 2 and 3 fo gende ca ego ie and emo ion ca ego ie , e pec i el .

B ain eg ionTal co o dina e ma eigh N mbe of o el in he cl e Le P ecen al G 51 1300.0924

Brain region	Tal coordinates			max weight	Numbers of voxels in the clusters
	x	y	z		
Righ P ec ne ,	12	−50	52	0.087	23
Le Middle F on al G ,	−38	36	30	0.067	26
Righ Middle F on al G ,	40	27	43	0.084	32
Righ Middle Tempo al G ,	60	−21	−10		
					38 36 21

($p < 10^{-9}$, F(2, 8) = 36.97 fo gende ca ego ie ; $p < 10^{-11}$, F(2, 8) = 46.13 fo emo ion ca ego ie). F he mo e, po hoc Bonfe oni-co ec ed pai ed - e demon a ed ha he c o - ep od cibili a io e e igni can l highe fo he ele an a k han fo he i ele an a k (gende ca ego ie : $p < 0.001$ co ec ed, (8) = 16.23 fo gende a k . n mbe a k; $p < 0.001$ co ec ed, (8) = 15.49 fo gende a k . emo ion a k; emo ion ca ego ie : $p < 0.001$ co ec ed, (8) = 16.05 fo emo ion a k . n mbe a k; $p < 0.001$ co ec ed, (8) = 14.36 fo emo ion a k . gende a k) and ha he e a no igni can di e ence be een he n mbe a k and he i ele an emo- ion/gende a k (all $p > 0.05$) (Fig. 4). Ba ed on he e of info ma i e o el fo he gende /emo ion ca ego ie , e al o pe fo med gende ca ego and emo ion ca ego decoding fo each of he a dio i al n i h n mbe , gende and emo ion a k ; he co e ponding c o -decoding acc ac a e a e p e en ed in Fig. S6. F om Table 2 and 3 and Fig 3 and S6, e can concl de he follo ing: (i) he info ma i e o el in Table 2/Table 3 a e in ol ed in he p oce ing of he gende /emo ion fea e in he a dio i al condi ion ; (ii) he co e ponding o el in Table 2/Table 3 a e info ma i e onl hen he gende /emo ion fea e i a ended.

Fo he p po e of f nc ional connec i i calc la ion, e elec ed fo o el cl e each i h i e 62 f om he he e omodal a ea le STS/MTG (cl e cen e : (−52 −22 8)), igh STS/MTG (cl e cen e : (54 −18 9)), le pe i hinal co e (cl e cen e : (−26, −20, −22)), and igh pe i hinal co e (cl e cen e : (26, −18, −22)), a de c ibed in he ela ed efe ence [10,32]. Fo each of he a dio i al n i h n mbe , gende and emo ion a k , e calc la ed he f nc ional connec i i i h o di ec ion be een he he e omodal a ea and he info ma i e b ain a ea in Table 2 (fo gende ca ego ie) o Table 3 (fo emo ion ca ego ie) ia G ange ca ali anal i a

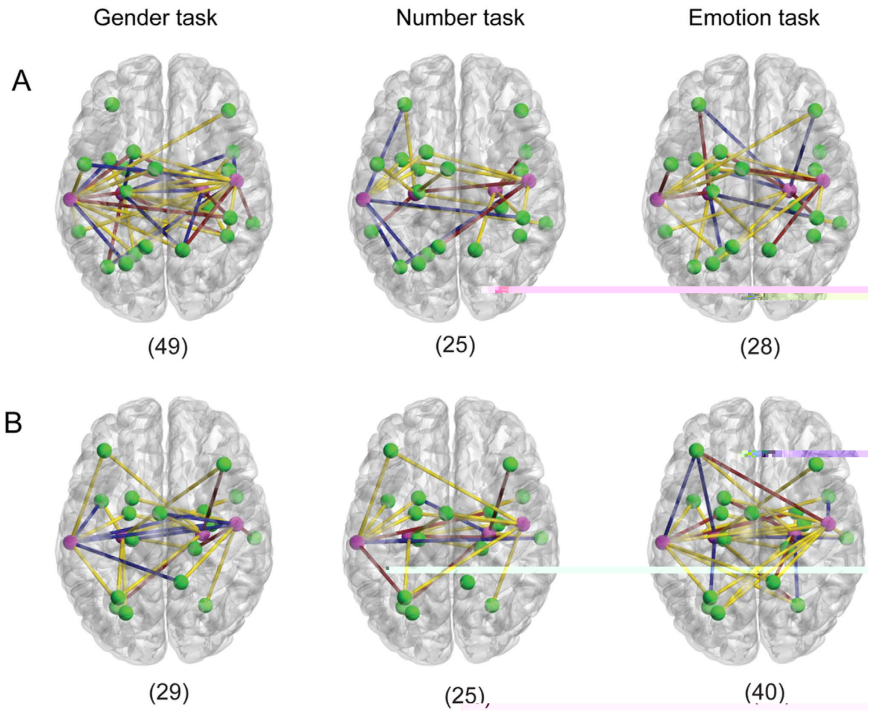

Figure 5. The functional connectivity between the heteromodal areas and the brain areas encoding the gender feature (A) or the emotion feature (B). G een phe e : b ain a ea f om Table 2 in (**A**) o Table 3 in (**B**). Magen a phe e : he e omodal a ea . Yello line : connec ion f om he he e omodal a ea o he info ma i e b ain a ea . Bl e line : connec ion f om he info ma i e b ain a ea o he he e omodal a ea . P ple line : connec ion i h bi-di ec ion. N mbe in b acke : o al n mbe of f nc ional connec ion .

he g o p le el (ee Ma e ial and Me hod). A ho n in Fig. 5, he e e e mo e f nc ional connec ion f om he he e omodal a ea o he b ain a ea encoding he gende /emo ion fea e (Table 2/Table 3) fo he ele an a k (gende /emo ion a k) han fo he i ele an a k (n mbe and emo ion/gende a k). We h ob e ed ha in he a dio i al condi ion, fea e- elec i e a en ion enhanced he f nc ional connec i i and h eg la ed he info ma ion o f om he he e omodal a ea o he b ain a ea encoding he a ended fea e. F he mo e, hi enhancemen of he f nc ional connec i i ma impl ha bo h he he e omodal a ea and he b ain a ea encoding he a ended fea e a e in ol ed in a dio i al eman ic in eg a ion.

Discussion. In he p e en d , e e plo ed he ne al mod la ion of a dio i al eman ic in eg a ion b fea e- elec i e a en ion. D ing he fMRI e pe imen , he bjec e e in c ed o neglec all fea e , a end o a ingle fea e (gende o emo ion), o im l aneo l a end o o fea e (bo h gende and emo- ion) of a e ie of facial mo ie clip in he i al-onl , a di o -onl and a dio i al im l condi ion . To a e he eman ic info ma ion of a fea e encoded in he b ain, e calc la ed a ep od cibili a io fo each fea e, e pe imen al a k and im l condi ion b appl ing an MVPA me hod o he fMRI da a, and e f he anal ed he f nc ional connec i i be een he b ain a ea encoding he eman ic fea e and he he e omodal a ea . O e l gge ed ha in he a dio i al condi ion, fea e- elec i e a en ion ma f nc ion a a p e- eq i i e fo he a dio i al eman ic in eg a ion of a fea e and ha he h man b ain migh elec i el in eg a e he eman ic info ma ion of he a ended fea e b enhancing he f nc ional connec i i and h in encing he info ma ion o f om he he e omodal a ea o he b ain a ea encoding he fea e. F he mo e, he ep od cibili a io ma e e a an inde fo e al a ing he a dio i al eman ic in eg a ion of a fea e.

Feature-selective attention: enhancing the neural representations of the attended features in the audiovisual condition. Con ide ing he a dio i al condi ion i h n mbe , gende , emo ion, and bi-fea e a k , e ob e ed ha he ep od cibili a io and decoding acc ac a e e e highe fo he a ended fea e han fo na ended fea e (Fig 3 and 4, S4–S6). i e l indica e ha fea e- elec i e a en ion enhanced he ne al ep e en a ion of he a ended fea e and h inc ea ed bo h he imila i of he ne al ac i i pa e n i hin a cla (e.g., male o female cla) and he di e ence be een he o cla e of he ne al ac i i pa e n (e.g., male . female). To foc on ele an info ma ion and igno e ha i i ele an , he h man b ain i eq ipped i h a elec ion mechani m accompli hed b he cogni i e f nc ion of a en ion[34]. Speci call , in he i al-onl o a di o -onl condi ion, he b ain elec i el p oce e one o e e al fea e ia fea e- elec i e a en ion[7,9,15–17]. O e l e ealed ha in he a dio i al condi ion, he fea e- elec i e a en ion mechani m ill pe mi elec i e p oce ing of he a ended fea e . In con a o he i al-onl o a di o -onl condi ion, fea e- elec i e a en ion in he a dio i al condi ion elec i el enhanced he

f nc ional connec i i f om he he e omodal a ea and he b ain a ea encoding he a ended fea e (Fig. 5). i enhancemen mod la ed he co e ponding info ma ion o , and pla ed an impo an ole in achie ing he enhancemen of ne al ep e en a ion of he a ended fea e in he a dio i al condi ion.

Feature-selective attention: a prerequisite for the audiovisual integration of a semantic feature. Fi , o da a anal i e l fo he e pe imen al n i h he n mbe a k ppo ed he concl ion ha fea e- elec i e a en ion i a p e eq i i e fo he a dio i al in eg a ion of a eman ic fea e. A ho n in Fig. 2 (A,E), hen none of he fea e of he a dio i al im li e e a ended, a dio i al en o in eg a- ion a no ob e ed, no o men ion highe le el a dio i al eman ic in eg a ion. Second, ing he da a fo he a dio i al n i h he bi-fea e a k, e epa a el locali ed he b ain a ea a ocia ed i h he gende and emo ion ca ego di e en ia ion (Table 2 and 3, e pec i el). P e io die ha e demon a ed ha ome of he elec ed b ain a ea , peci call he STS and he f ifo m g , a e in ol ed in facial info ma- ion p oce ing[35 38]. Fo each of he a dio i al n i h he n mbe , gende and emo ion a k , e calc la ed c o - ep od cibili a io and c o -decoding acc ac a e fo he gende and emo ion fea e ing he elec ed o el in Table 2 and 3. We h demon a ed ha he e o el encoded he eman ic info ma ion of a fea e (gende o emo ion) onl hen he fea e a a ended (Fig 4 and S6). A di ib ed ne o k incl ding he do al medial pe io empo al and en al in apa ie al a ea i in ol ed in he m l i en o in eg a ion of i al and e ib la info ma ion[39]. Acco dingl , e infe ha he a dio i al eman ic in eg a ion co e pond- ing o a fea e migh be accompli hed b a di ib ed ne o k incl ding he he e omodal a ea and he b ain a ea encoding he fea e (Fig. 5). When a fea e of an a dio i al objec i no a ended, o e l indica e ha he co e ponding info ma i e b ain a ea a e no in ol ed in he p oce ing of hi fea e (Fig 4 and S6), po en iall inhibi ing he a dio i al eman ic in eg a ion fo hi na ended fea e.

Feature-selective audiovisual semantic integration. In hi d , f om he pe pec i e of ne al info ma ion encoding and f nc ional connec i i , e demon a ed he mod la ion e ec of fea e- elec i e a en ion on a dio i al eman ic in eg a ion. Speci call , hen one o o fea e of he a dio i al objec e e a ended, he enhancemen of he ne al e pon e le el in he he e omodal a ea of he pSTS/MTG indi- ca ed he occ ence of a dio i al en o in eg a ion (Fig. 2B D,F H), p o iding he ba i fo he a dio i - al eman ic in eg a ion co e ponding o he a ended fea e . MVPA anal i demon a ed ha fo onl he a ended fea e , he eman ic info ma ion encoded in he b ain a imp o ed b he a dio i al im li compa ed i h he i al-onl and he a di o -onl im li (Fig 3, S4, and S5). We p e io l con ide ed he ca e in hich a ingle fea e of he im li a a ended[22], a in he e pe imen i h he gende and emo ion a k in hi d . Compa ed i h he i al-onl and a di o -onl im l condi ion , e ob e ed ha he cong en a dio i al im li enhanced he ne al ep e en a ion of he a ended fea e . Ho e e , ho hi enhancemen i implemen ed in he b ain emain nclea . In hi d , e e ended hi concl ion fo he ca e in hich none of he fea e a a ended o mo e han one fea e of he im l a a ended. F he mo e, he G ange ca al connec i i anal i indica ed ha no onl he he e omodal a ea b al o he b ain a ea encoding he a ended fea e ma be in ol ed in he a dio i al eman ic in eg a ion. In he a dio i al con- di ion, fea e- elec i e a en ion enhanced/ ed ced he f nc ional connec i i f om he he e omodal a ea and he b ain a ea encoding he a ended/ na ended fea e (Fig. 5) and he efo e mod la ed he info ma ion o among he e a ea . i mod la ion ma be e pon ible fo he enhancemen of he eman ic info ma ion of he a ended fea e b he a dio i al im li. o gh hi mod la ion of fea e- elec i e a en ion, he h man b ain ma elec i el in eg a e he eman ic info ma ion fo he a ended fea e of he a dio i al facial im li. B con a , fo he na ended fea e , he co e ponding a dio i al eman ic in eg a ion a inhibi ed.

Reproducibility ratio: an index for the audiovisual semantic integration of a feature. To fo m high-le el concep al ep e en a ion of he eman ic fea e of an a dio i al objec , he b ain pe fo m a dio i al eman ic in eg a ion, hich ma be ba ed on a dio i al in eg a ion a he en o le el[10]. N me o ne oimaging and elec oph iological die ha e demon a ed ha cong en a dio i al im li can enhance ne al ac i i ie , e.g., in he bila e al pe io empo al g (STG)[18 21]. Con e el , in he a dio i al condi ion, he enhancemen of b ain ac i i ie in he e omodal a ea ch a he pSTS/MTG ma e e a an indica o of a dio i al en o in eg a- ion[4,24 26]. Rega ding a dio i al eman ic in eg a ion, n me o die ha e di c ed he in ence of eman ic fac o on a dio i al in eg a ion (ee efe ence[40] and he efe ence he ein). Ho e e , no die ha e add e ed he di e en ia ion of he e ec of a dio i al eman ic in eg a ion fo di e en eman ic fea e . e di c l ma lie in he a e men of he in eg a ed and nin eg a ed info ma ion con ained in he b ain ignal . In hi d , e ob e ed ha he a dio i al eman ic in eg a ion e ec a ocia ed i h di e en fea e- elec i e a en ion a k co ld no be di e en ia ed ba ed on he le el of ne al ac i i ie in he pSTS/MTG (ee Re l and Fig. 2). i e l i con i en i h he f nc ion of he pSTS/MTG a a p e eman ic, he e omodal egion fo c o modal pe cep al fea e [10]. MVPA app oache open he po ibili of epa a ing and locali ing pa iall di ib ed pa e n , hich gene all a e oo eak o be de ec ed b ni a ia e me hod ch a GLM[23,41 43]. U ing an MVPA me hod, e calc - la ed a ep od cibili a io co e ponding o a fea e o a e he eman ic info ma ion encoded in he b ain; he co e ponding eman ic info ma ion a enhanced onl fo he a ended fea e hen he a dio i al im l con- di ion a compa ed i h he i al-onl and a di o -onl im l condi ion (Fig 3, S4 and S5). We h ob e ed he di e en ial e ec of a dio i al eman ic in eg a ion fo he a ended and na ended fea e . F he mo e, he ep od cibili a io migh be ed a an inde fo e al a ing he a dio i al eman ic in eg a ion of a fea e.

Finall , e de c ibe e e al limi a ion of hi d o ill a e f e di ec ion . Fi , e emplo ed a ela i el comple e pe imen al de ign, hich led o he collec ion of la ge amo n of da a. Fo each bjec , he collec ion of he f nc ional and c al MRI da a la ed abo i ho , no incl ding p epa a ion ime. Beca e of he di c l in da a collec ion, e ed a ela i el mall n mbe of bjec . B a i icall igni can e pe imen al

e l e e ill ob ained. Second, onl i al-onl , a di o -onl and a dio i al facial im li e e con ide ed in hi d . In he f e, e m , implif o e pe imen al de ign, inc ea e he n mbe of bjec , and f he con ide non-facial im li o e end o concl ion .

References

1. Cal e , G. A. & e en, T. M l i en o in eg a ion: me hodological app oache and eme ging p inciple in he h man b ain. *J. Physiol. Paris* **98,** 191 205 (2004).
2. Campanella, S. & Belin, P. In eg a ing face and oice in pe on pe cep ion. *Trends Cogn. Sci.* **11,** 535 543 (2007).
3. Sch einbe ge , S. ., obe on, D. & a fmann, J. M. Hea ing facial iden i ie . *Q. J. Exp. Psych.* **60,** 1446 1456 (2007).
4. B ha a, . O. *et al.* Ne al co ela e of c o -modal binding. *Nat. Neurosci.* **6,** 190 195 (2003).
5. Macal o, E., F i h, C. D. & D i e , J. M l i en o im la ion i h o i ho accade : fM I e idence fo c o modal e ec on en o - peci c co ice ha e ec m l i en o loca ion-cong ence a he han a - ele ance. *NeuroImage* **26,** 414 425 (2005).
6. Macal o, E., Geo ge, N., Dolan, ., Spence, C. & D i e , J. Spa ial and empo al fac o d ing p oce ing of a dio i al peech: a PET d . *NeuroImage* **21,** 725 732 (2004).
7. McCl in, J. W. & Op ican, L. M. P ima e ia e and p e ia e co ical ne on d ing di c imina ion. I. Sim l aneo empo al encoding of info ma ion abo colo and pa e n. *J. Neurophysiol.* **75,** 481 495 (1996).
8. Nob e, A. C., ao, A. & Chela i, L. Selec i e a en ion o peci c fea e i hin objec : Beha io al and elec oph iological e idence. *J. Cognitive Neurosci.* **18,** 539 561 (2006).
9. Woodman, G. F. & Vogel, E. . Selec i e o age and main enance of an objec ' fea e in i al o ing memo . *Psychon. B. Rev.* **15,** 223 229 (2008).
10. Ta lo , . I., Mo , H. E., S ama a i , E. A. & T le , L. . Binding c o modal objec fea e in pe i hinal co e . *Proc. Natl. Acad. Sci. U.S.A.* **103,** 8239 8244 (2006).
11. Tal ma, D., Sen o i, D., So o-Fa aco, S. & Woldo , M. G. e m l iface ed in e pla be een a en ion and m l i en o in eg a ion. *Trends Cogn. Sci.* **14,** 400 410 (2010).
12. Le i , J. W., Bea champ, M. S. & DeYoe, E. A. A compa i on of i al and a di o mo ion p oce ing in h man ce eb al co e . *Cereb. Cortex* **10,** 873 888 (2000).
13. Joa in, F. *et al.* C o -modal in e ac ion be een h man face and oice in ol ed in pe on ecogni ion. *Cortex* **47,** 367 376 (2011).
14. Sai o, D. N. *et al.* C o -modal binding and ac i a ed a en ional ne o d ing a dio- i al peech in eg a ion: a f nc ional M I d . *Cereb. Cortex* **15,** 1750 1760 (2005).
15. Ah eninen, J. *et al.* Ta -mod la ed ha and he e pa h a in h man a di o co e . *Proc. Natl. Acad. Sci. USA.* **103,** 14608 14613 (2006).
16. Ma n ell, J. H. . & Hoch ein, S. E ec of beha io al a e on he im l elec i i of ne on in a ea V4 of he macaq e mon e . In: Channel in he i al ne o em: ne oph iolog , p choph ic and model , (ed, Bl m B), 447 470. London: F e nd (1991).
17. Mi abella, G. *et al.* Ne on in a ea V4 of he macaq e an la e a ended i al fea e in o beha io all ele an ca ego ie . *Neuron* **54,** 303 318 (2007).
18. Jeong, J. W. *et al.* Cong ence of happ and ad emo ion in m ic and face modi e co ical a dio i al ac i a ion. *NeuroImage* **54,** 2973 2982 (2011).
19. eifel , B., E hofe , T., G odd, W., E b, M. & Wildg be , D. A dio i al in eg a ion of emo ional ignal in oice and face: an e en - ela ed fM I d . *Neuroimage* **37,** 1445 1456 (2007).
20. M lle , V. I., Cie li , E. C., T e , B. I. & Eic ho , S. B. C o modal in e ac ion in a dio i al emo ion p oce ing. *Neuroimage* **60,** 553 561 (2011).
21. M lle , V. I. *et al.* Incong ence e ec in c o modal emo ional in eg a ion. *Neuroimage* **54,** 2257 2266 (2011).
22. Li, Y. *et al.* C o modal In eg a ion Enhance Ne al ep e en a ion of Ta - ele an Fea e in A dio i al Face Pe cep ion. *Cereb. Cortex* **25,** 384 395 (2015).
23. F i on, . J. *et al.* S a i ical pa ame ic map in f nc ional imaging: a gene al linea app oach. *Hum. Brain Mapp.* **2,** 189 210 (1994).
24. Cal e , G. A., Campbell, . & B amme , M. J. E idence f om f nc ional magne ic e onance imaging of c o modal binding in he h man he e omodal co e . *Curr. Biol.* **10,** 649 657 (2000).
25. F a ine i, F., Bolognini, N. & La, d. E. Enhancemen of i al pe cep ion b c o modal i o-a di o in e ac ion. *Exp. Brain Res.* **147,** 332 343 (2002).
26. Macal o, E. & D i e , J. M l i en o pa ial in e ac ion : a indo on o f nc ional in eg a ion in he h man b ain. *TRENDS Neurosci.* **28,** 264 271 (2005).
27. Bea champ, M. S. S a i ical c i e ia in FM I die of m l i en o in eg a ion. *Neuroinformatics* **3,** 93 113 (2005).
28. B e , M., An on, J.-L., Valab eg e, . & Poline, J.-B. egion of in e e anal i ing he Ma Ba oolbo fo SPM 99. *Neuroimage* **16,** 1140 1141 (2002).
29. iege o e, N., Goebel, . & Bande ini, P. Info ma ion-ba ed f nc ional b ain mapping. *Proc. Natl. Acad. Sci. USA.* **103,** 3863 3868 (2006).
30. Nichol , T. & Ha a a a, S. Con olling he famil i e e o a e in f nc ional ne oimaging: a compa a i e e ie . *Stat. Methods Med. Res.* **12,** 419 446 (2003).
31. Hamil on, J. P., Chen, G., oma on, M. E., Sch a , M. E. & Go lib, I. H. In e iga ing ne al p imac in Majo Dep e i e Di o de : m l i a ia e G ange ca ali anal i of e ing- a e fM I ime- e ie da a. *Mol. Psychiatry* **16,** 763 772 (2011).
32. Hop nge , J. B., B onoco e, M. H. & Mang n, G. . e ne al mechani m of op-do n a en ional con ol. *Nat. Neurosci.* **3,** 284 291 (2000).
33. Se h, A. . A MATLAB oolbo fo G ange ca al connec i i anal i . *J. Neurosci. Meth.* **186,** 262 273 (2010).
34. Tal ma, D., Do , T. J. & Woldo , M. G. Selec i e a en ion and a dio i al in eg a ion: i a ending o bo h modali ie a p e eq i i e fo ea l in eg a ion? *Cereb. Cortex* **17,** 679 690 (2007).
35. Gobbini, M. I. & Ha b , J. V. Ne al e pon e o he i al familia i of face . *Brain Res. Bull.* **71,** 76 82 (2006).
36. Ha b , J. V., Ho man, E. A. & Gobbini, M. I. e di ib ed h man ne al em fo face pe cep ion. *Trends Cogn. Sci.* **4,** 223 232 (2000).
37. Ha b , J. V. *et al.* Face encoding and ecogni ion in he h man b ain. *Proc. Natl. Acad. Sci. USA* **93,** 922 927 (1996).
38. Le e oni, C. L. *et al.* Ne al em nde l ing he ecogni ion of familia and ne l lea ned face . *J. Neurosci.* **20,** 878 886 (2000).
39. Zhang, W. & W , S. ecip ocall Co pled Local E ima o Implemen Ba e ian Info ma ion In eg a ion Di ib i el . in *Adv. Neural Infor. Processing Syst.* (ed C.J.C. B ge , L. Bo o , M. Welling, Z. Ghah amani & .Q. Weinbe ge) **26,** 19 27 (2013).
40. Doeh mann, O. & Na me , M. J. Seman ic and he m l i en o b ain: ho meaning mod la e p oce e of a dio- i al in eg a ion. *Brain Res.* **1242,** 136 150 (2008).
41. Goebel, . & an A e eld , N. M l i en o f nc ional magne ic e onance imaging: a f e pe pec i e. *Exp. Brain Res.* **198,** 153 164 (2009).
42. Pe ei a, F., Mi chell, T. & Bo inic , M. Machine lea ning cla i e and fM I: a o ial o e ie . *Neuroimage* **45,** 199 209 (2009).
43. Pol n, S. M., Na , V. S., Cohen, J. D. & No man, . A. Ca ego - peci c co ical ac i i p ecede e ie al d ing memo ea ch. *Science* **310,** 1963 1966 (2005).

Acknowledgements

i o k a , ppo ed b he Na ional Ke Ba ic Re ea ch P og am of China (973 P og am) nde G an 2015CB351703, he Na ional High- ech R&D P og am of China (863 P og am) nde G an 2012AA011601, he Na ional Na al Science Fo nda ion of China nde G an , 91420302, 81471654 and 61403147, and G angdong Na al Science Fo nda ion nde G an 2014A030312005.

Author Contributions

Y.L. de igned e ea ch and o e he pape ; J.L. and W.W. anal ed he da a; B.H., T.Y. and P.L. pe fo med he e ea ch; F.F. and P.S. e i ed he pape ; all a ho , e ie ed he man c ip .

Additional Information

Supplementary information accompanie hi pape a h p:// .na e.com/ ep

Competing financial interests: e a ho declа e no compe ing nancial in e e .

How to cite this article: Li, Y. *et al.* Selec i e A dio i al Seman ic In eg a ion Enabled b Fea e-Selec i e A en ion. *Sci. Rep.* **6**, 18914; doi: 10.1038/ ep18914 (2016).