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Selective Audiovisual Semantic Integration Enabled by Feature-Selective Attention

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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 information f ows from heteromodal areas to brain areas encoding the attended features.

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 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 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.

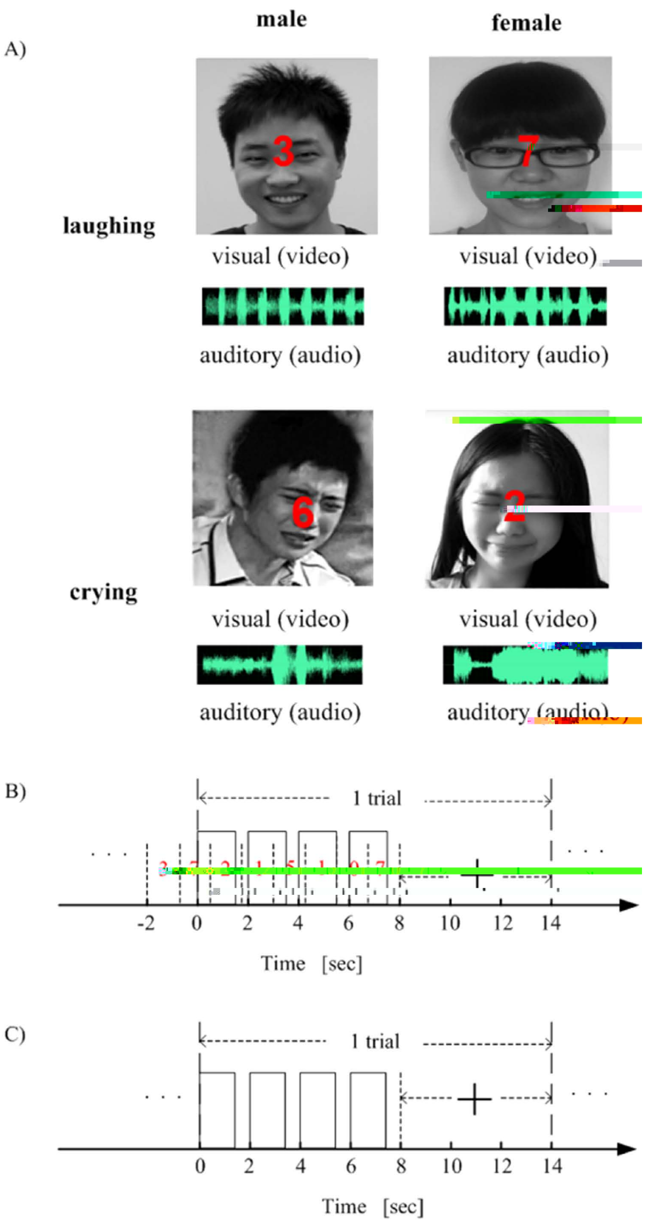

Figure 1. Experimental stimuli and time courses. (**A**) Fo e ample of a dio i al im li; he ed n mbe indica e n i h he n mbe a k onl . (**B**) Time co e of a ial fo he n i h he n mbe a k, in hich he im li incl ded andoml p e en ed n mbe and ideo /a dio /mo ie clip . (**C**) Time co e of a ial fo he n 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 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 he e $\theta_{i,j}$ i he angle be een o pa e n ec o P_i

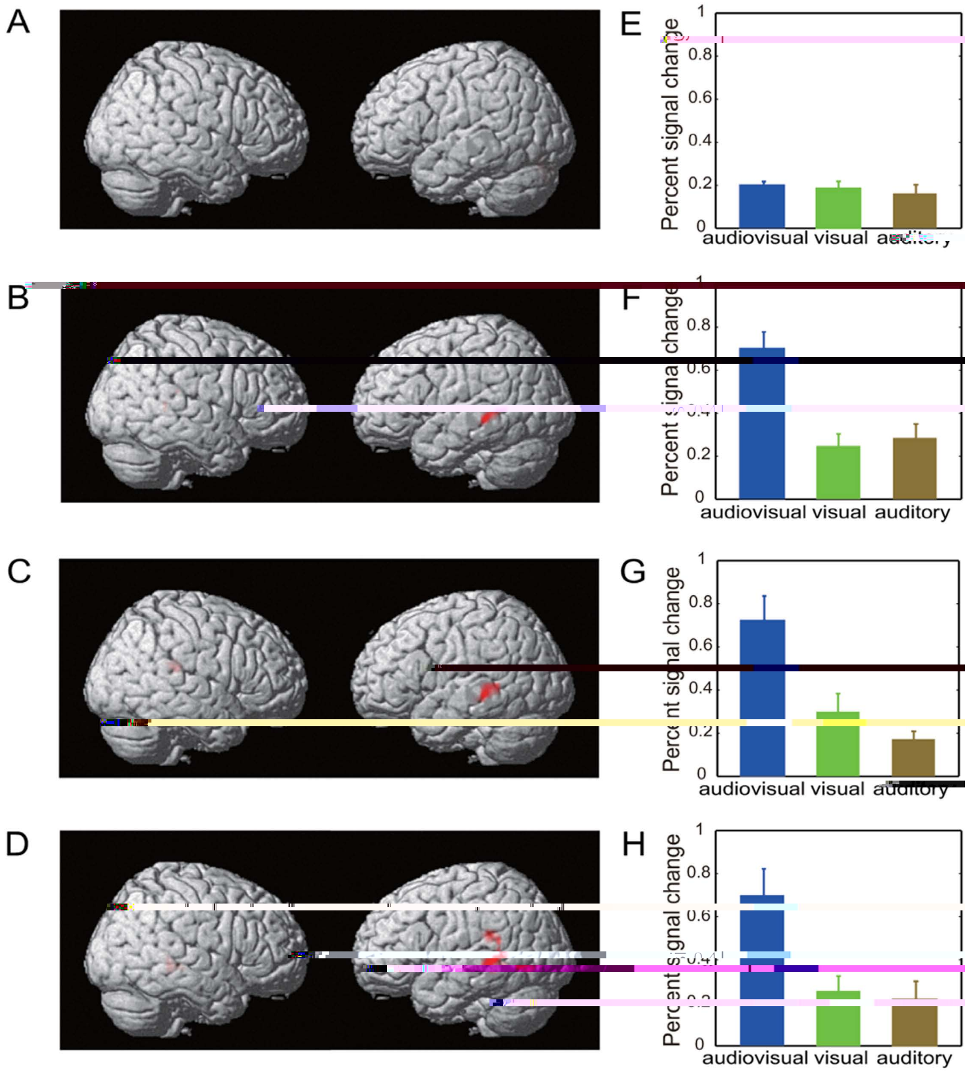

Figure 2. Brain areas for audiovisual sensory integration that met the criterion [AV>max (A,V) ($p < 0.05$, FWE-corrected)]∩[V>0 or A>0 ($p < 0.05$, uncorrected)]. (**A**) No b ain a ea e hibi ed a dio i al en o in eg a ion fo he n mbe a k. (**B**) B ain a ea e hibi ing a dio i al en o in eg a ion fo 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 egoie (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 : $p < 10^{-11}$, $F(2, 8) = 88.73$; 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 :

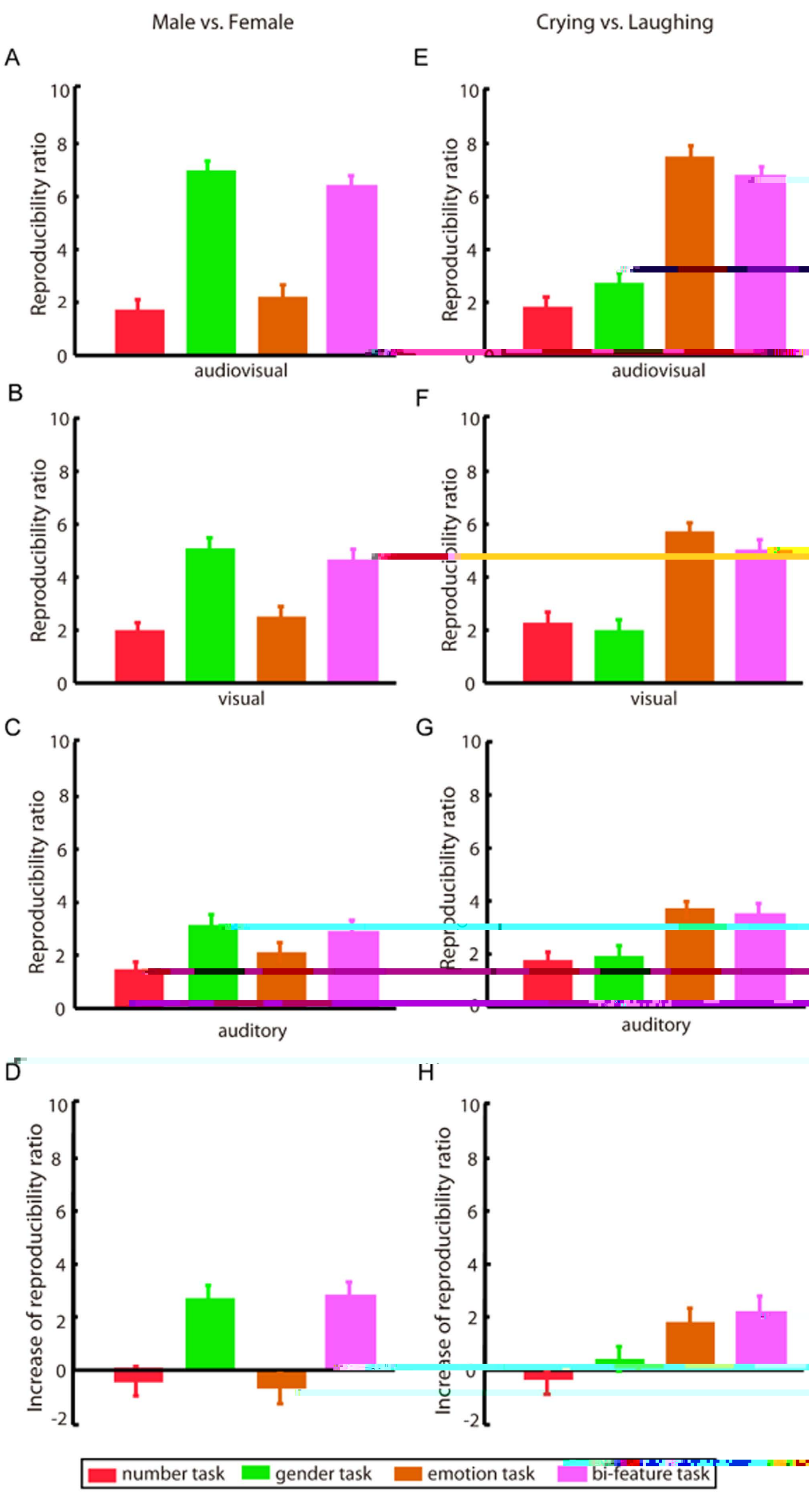

Figure 3. Reproducibility ratios (means and standard errors across all subjects) and the corresponding comparison results. Le /Righ : gende /emo ion ca ego ie ; he 3 o : a dio i al, i al-onl and a di o -onl im l condi ion , e pec i el ; he 4 h o : he ep od cibili a io in he a dio i al condi ion min he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

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	3210		
Le Midd a2.4(e 9(l i5(l G)19.1(p)-9(o)12(a)-5(l G)8( )-3( )-)120( )3( )]TJ/T1 1 Tf0 T			17.332 0 Td( )Tj/T1 1 Tf-0.185 T	/Span Ac alTe EFF200A BDC ( )TjEMC (38)Tj0 T4 4.55	

($p < 10^{-9}$, $F(2, 8) = 36.97$ 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

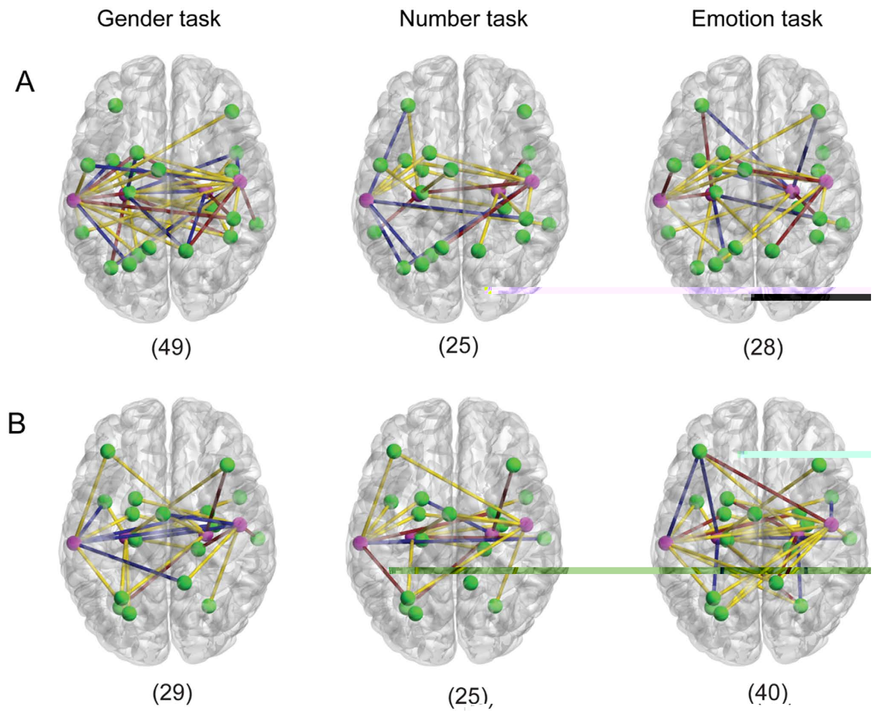

Figure 5. The functional connectivity between the heteromodal areas and the brain areas encoding the gender feature (A) or the emotion feature (B). G een phe e : b ain a ea f om Table 2 in (**A**) o Table 3 in (**B**). Magen a phe e : he e omodal a ea . Yello line : connec ion f om he he e omodal a ea 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 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 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[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 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 .

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Y.L. designed research and wrote the paper; J.L. and W.W. analyzed the data; B.H., T.Y. and P.L. performed the research; F.F. and P.S. revised the paper; all authors reviewed the manuscript.

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