d :10.1093/b a /a 299 B a 2011: 134; 235 246 235

BRAIN
A JOURNAL OF NEUROLOGY

Neural representation of self-concept in sighted and congenitally blind adults

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C : S Ha , P D,
a_ P c ,
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5 Y a R ad,
100871,
' b c C a
E- a : a @ d .c

The functional organization of human primary visual and auditory cortices is influenced by sensory experience and exhibits cross-modal plasticity in the absence of input from one modality. However, it remains debated whether the functional architecture of the prefrontal cortex, when engaged in social cognitive processes, is shaped by sensory experience. The present study investigated whether activity in the medial prefrontal cortex underlying self-reflective thinking of one's own traits is modality-specific and whether it undergoes cross-modal plasticity in the absence of visual input. We scanned 47 sighted participants and 21 congenitally blind individuals using functional magnetic resonance imaging during trait judgements of the self and a familiar other. Sighted participants showed medial prefrontal activation and enhanced functional connectivity between the medial prefrontal and visual cortices during self-judgements compared to other-judgements on visually but not aurally presented trait words, indicating that medial prefrontal activity underlying self-representation is visual modality-specific in sighted people. In contrast, blind individuals showed medial prefrontal activation and enhanced functional connectivity between the medial prefrontal and occipital cortices during self-judgements relative to other-judgements on aurally presented stimuli, suggesting that visual deprivation leads to functional reorganization of the medial prefrontal cortex so as to be tuned by auditory inputs during self-referential processing. The medial prefrontal activity predicted memory performances on trait words used for self-judgements in both subject groups, implicating a similar functional role of the medial prefrontal cortex in self-referential processing in sighted and blind individuals. Together, our findings indicate that self-representation in the medial prefrontal cortex is strongly shaped by sensory experience.

Keywords: a a c ; ; c a_ a c a _ a ; da a c ; b d
Abbreviation: BA = B d a a; MRI = a c a _ a

Introduction

a a c ab _ a b a c a c a c d a ada _ a (Ba a d , 2002; Pa c a *et al*., 2005). S d _ a a d- a a o a d _ d a c _ a a a d d c b . T cc a c a c_ d a d _ a ac a d b a d d / d (B *et al*., 2002; G *et al*., 2009) a d b B a ad b d d d a (Sada *et al*., 1996; B c *et al*., 1998; B *et al*., 2002). M , cc a ac a b d d d a dc b a a _ a a d

d J 1, 2010. d b 2, 2010. Ac d b 5, 2010. Ad a Ac b ca N b 4, 2010

F , a a : a : @ d a .

a . c a d ca a (G *et al*., 2005) a d ba- (A d *et al*., 2003). S a , a d a c a a d c b ac (E a *et al*., 1998) a d a a (N a *et al*., 1999) a . T d dca a b a a a c a c ada c a, a d ac a .

H , b a a d c a a- a c ca c d ca c à à d b c à c . T aac- à c d b a a d a d ca ' c ca (Ka *et al*., 2003). T c , c d b d a ac a d a ac (R a a d S a a, 2010), ac à d b d d d b ac b d a d c a b d d a (R cc a d *et al*., 2009). T à a c a a d b c a à a b d a c a b d a c a (B d *et al*., 2009). T , a a a b a à c a c a d a da a d a . A a a a , a a a ab a a a b a c ca c a ab ' d a d a- a a a a . a a d ' a a d a d c a b d ad (B d *et al*., 2009).

I c a a da c c a ac d c a d . S a a ca a a a d a d ca d a d da- a (B a a *et al*., 1999). M a ' a ac à da ac (Ca d a a d , 2006), c , , à d ' a (S a *et al*., 2008). T à b a c a c à d à d c a b da - c a d à d b d d - c . M , a b à d b a- a ac c d a à b c a a d a d a a ac c .

T c add d b a a ac da a c à d -c a (N a d , 2004) da - c c a d à d b . W da a a a a d (R *et al*., 1977), a d ca b c d d b a a d a d da . I a b a da a ac à a d (K *et al*., 2002; L a *et al*., 2004; M c *et al*., 2006; Z *et al*., 2007) a d à a - c a d a d a - c a d (Mac a *et al*., 2004; M a *et al*., 2006), a a da a c -c a . H , d d à d da a ac a d a d ac a d a c ac a da - c c, a d , a a ad a a da a c c a b d a d da d a c . T d, b a a d a da a a d a (J *et al*., 2002). T d d à d ac a- c a - d a . d d da a c , c a a ca d a a a a . d . H , dd c a - d , a a a a da a c à a a a d .

Acc d a -c c d a ab ac b c . d (B d a d S , 1997; K *et al*., 2003), a ac -c a d a a b a a a . H , a b a -c a a d b a d (G b , 1979; B , 1992) a d a d a da a , c a à c a ac a d b d a (B d a d C , 1998; à *et al*., 2007). I c -c a ba a ' a , a a da a ac à d -c a a d d a a a d da . I add , da a ac a d à b a d da b d d d a a d , a a a, d à d c b a d a d a a c c ' -c .

T , E 1 ca d d a c- a c a MRI d d a a d a d ab ' a , a a a ' a , a d d à c . S a d (*et al*., 2002; a *et al*., 2004; M c *et al*., 2006; Z *et al*., 2007), c a - d a d - d a d a ac -c a a d c a - d a d a ac a c à d a ' a d (F . 1). A E 1 d a da a ac a a c à d a a c a da , E 2 ca d c a b d d d a a d d c d -, - a d à c - d a a d a ac. a ad c a a da a c a d d a d a c .

Materials and methods

Subjects

T - d a c a c d E 1. T d a c a c d da a a a d

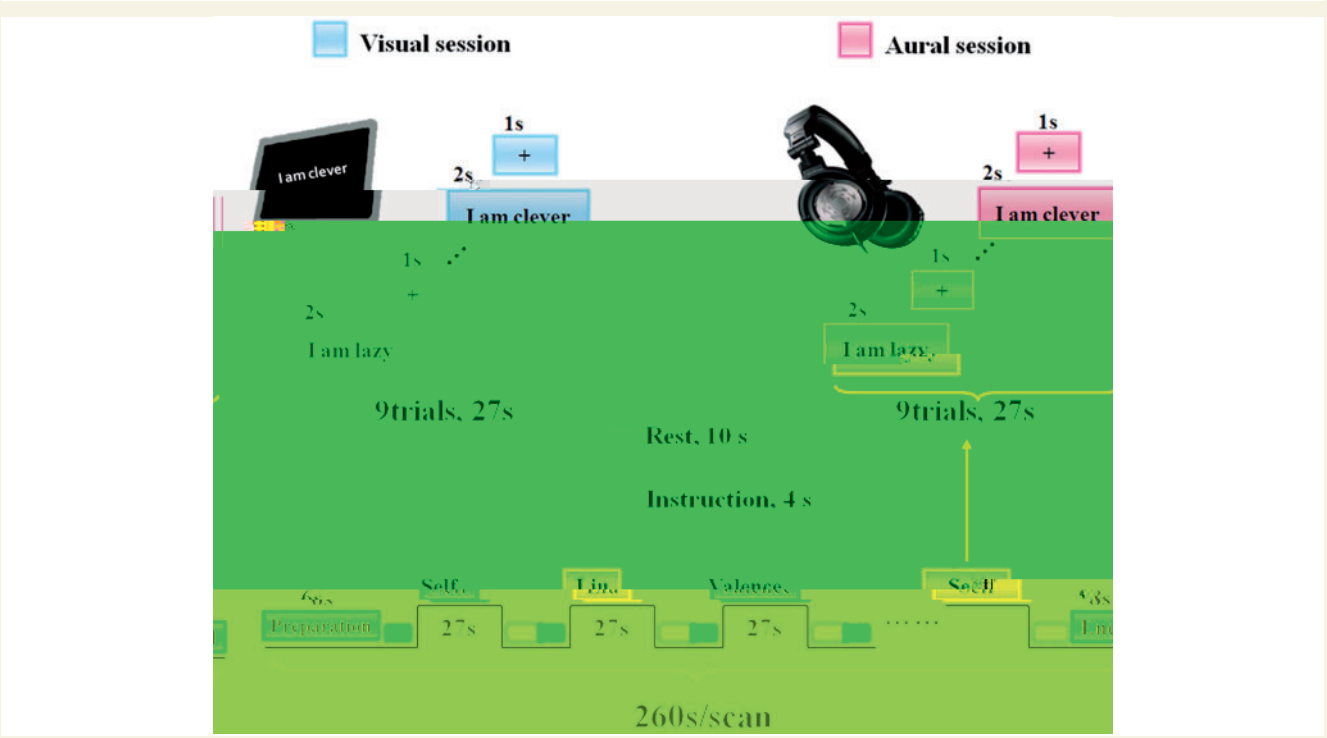

Figure 1 E a d E 1. A b c a d. B c a c d a d a c a c d a ad . T c a a d a d ca. Eac c d a a d a d b a 4 c a d d b a 10 a c . T a a d a a -, - a d a - d a d a d . Eac ca a d 260 .

ad . T a 23 d d d a (11 , 12 ; a a: 18 28 a a a =22.0 a) c d c a MRI da a a a . O b c a - a d, - a d. A d a c a - d ca c a c d a a d ad a c d- - a .

T - c a b d d d a a d 22 d c a c a c d E 2. T b d a d d c a c a c d da a a a d ad . Da a 19 c a b d a c a (11 , 8 ; a a: 18 28 a a a =25.2 a) a d 19 d c a c a (9 , 10 - ; a a: 19 28 a a a =23.2 a) c d c a MRI da a a a . O b d a c a a - a d a d - a d. A a c a ad ca c a c d a . T ca b d c d a a (*n* = 7), ca a ac (*n* = 5), a b - a a (*n* = 1), c a a (*n* = 2), a (*n* = 1), c a a (*n* = 1) a d c a a c a (*n* = 2). I d c - , a d b a ca c c , a d d . I d c a b a d ba b d a c a .

Stimuli and procedure

I E 1, d d ca d c d C d a d c a d a c a a c , c a d a a d d ad-c , a a c a -c a b a c ad

(22.05 H , 16b a a , , G dWa P c). V a - c d a b ac bac - d a d a d d c d ad b a . Eac c d a ab , a a c d C a (X a L a b c a d X a L a b c), a a a d . T a - d a a d a d da d - ca c . S b c a d a / d - d . ., 'I a b a'), d - d . ., 'L X a a ') a d a - d . ., ' a a d') b b a . P ca , a c a ac a a a a . Eac d a d a , a b c . I ac ca , ac b c d c a ca (. a d / a - d , a d / a - d a d a d / a a - d). D ac ca d a a d a a a d , 54 a (a) ac c d . A 6 o 'T ab a , a c a a . ' ac ca . Eac 31 a d a 4 c (c d o a a d ad a d), d b a . Eac a c d a 2 a , d b a 1 a a . T d a d b 10 d c a c a d a a a bac o .

A a 444 a a c d _ ab d a a a c (L , 1990), ac c c d

C c a ac . Ha d ad c ,
a d _ a a . T d a d -
ad c ad_ c b d 324 d_
a_ c a ca a d ad_ a d
54 d . T a _ ac c d a
c baa d ac b c . T d a d_
c b a a d d a a
d. Eac C c a ac c a d ac
a_ b d a a a 0.34° × 0.45° (d ×)
a a d a e 80 c .
A ca c d , a c a a a d
a d c _ . S b c d
60 d a d (20 a d _ ac d_ a) a d_
c _ a a a a d 60 a d . T d
a a d a d _ a c baa e d ac
b c . Eac d a d d d a 2 a d a c a
d ca d d d a d b a b
.
T _ a d d E _ 2 _ a
d E _ 1, e a a d
c d. Pa c a d ca , ac
c d ac ca . S d a c a _ a d a
ac b c. a d ca e d .
A ca e d , b b d a c a a d dc -
_ d _ a a d a d .

Imaging procedure

A GE 3 T ca a a da d ad c a d ac b d
(BOLD) ad c - a a _ a
(64 × 64 × 32_ a 3.75 × 3.75 × 4_ _ ^{3} a a ,
_ = 2000 , c _ = 30 , a = 90°, d
= 24 × 24 c) b c _ a d_
a . . A T$_1$- d c a _ a (256 × 256 ×
128_ a a a a 0.938 × 0.938 × 1.4_ ^{3}, -
_ = 7.4 , c _ = 3 , _ = 450 ,
a = 20°) a b ac d.

Imaging analysis

SPM2 (W c T e N _ a , L d , UK)
a d da a a a . T c a _ a c o d
ad _ . S _ a a (a a ; *x*, *y*, *z* a d
a ; c , , a) c d a ca_ . T
a a _ ca _ a a c d _ a a d _ a
a d _ a d a d a d T$_1$ M a M ca
I (MNI) a . T _ a a a d
c a _ a , c a d 2 _ c
a d a a _ d a c Ga a
8 _ - d a - a _ _ . T _ a da a _ d
a b -ca c . S a ca a a SPM2 d a a c ca
a d _ c _ . I ac b c ,
a a d d a ac d
a a L a M acc d c d . A
c d (a d / a - d_ , a d / a -
d_ , a d / a a e - d_ a d)
c d _ . A b -ca c a d c
ca ca e d a c ac c d . T
_ a a c d a _ a a acc
a d a _ a a d c .
A a a a c d d E _ 1
a a _ da a c
a a a d a d _
d a c a . T _ da a c a d
a priori c a - d a a ad
5 _ e da MNI c d a 8, 56, 9 [B d a a (BA) 10]
ba d a d da a a c a d -
a d - d C a c a (Z *et al*., 2007).
T a a _ a a ca d -
d a ca c a d _ d a c a
a d b o d a a d - a a a a e (ANOVA)
M da (a a d) a d J d_ (- d_
- d_ - d_ a e -
d_) a - b c a ab .
Ra d_ c a a a c d o d ba d a ca
a a _ a _ ac d d a a c a a a
e. C a - - d_ a d -
a e - d_ a a d a d _ ca c a d. I
a a ba a d a d - a d
- d_ ac d _ da , -b a a ca
a a c a a a ca c a d c _ -
ac b M da (a a d) × J d_
(- d_ - d_) b ca c a c a
1 –1 –1 1 (a - d_ , a - d_ , a d
- d_ a d a d - d_). S a , a
b a a d a - a d a e - d_ ac
d _ da , ac b M da (a
a d) × J d_ (- d_ a e - d_)
a c _ d b ca c a a c a 1 –1 –1 1 (a
- d_ , a a e - d_ , a d - d_
a d a d a e - d_). Ac a
a d_ c a a a d a c d
a $P < 0.05$ (c o d _ c_ a).
A c ca ac a a (F *et al*., 1997) a
_ d a a ba a a d ca
o a d c a a (. o a d c a c c) _ da
a ac a d - d_ c_ a d
- d_ . T c d a a _ c -
a - - d_ d a a a d -
_ a . d d a d . T ac
d d a b c a a d a a 5 - _ - ad e d
a a a _ da a c . T _
ac ad, a d c -
ca ac a ca c a d a -b
d c _ a - c o d ac a d a
c c d d a a c - d_
- d_ . T c ca ac -
o d ac b c ca a ab (- d_
- d_) a d ac a _ c _ da
a c . T d d a c a _ a c c
c ca ac b _ da a
c a d b a a b b b o d
- a *t* . T a a d b a
c ac _ a ca d o a d c -

b a a a d a a a - a a a d _ d a c a E _ 1. T a a _ a a d d d a . cac a d a d b d ANOVA J d - d - d - d - d) a a d - b c a ab a d G (b d a c a d c) a a - b c a ab. Ra d c a a a c d d cac a c a - d - d a d _ . P c ca ac a a a c d d a b a a a d d a d c a c c _ da a c d - d c d - d b d d _ da a c ac c a - d - d .

Results

Experiment 1: Brain imaging of sighted participants

T acc ac a d a - a a a a d _ [88 82%, $F(1,22) = 8.45$, $P = 0.008$]. A 2 (M da : a a a) × 3 (J d : - , - , a d a - d) ANOVA c d c - c (_ a a a) d a ca _ a c M da [$F(1,22) = 6.965$, $P = 0.015$], a b c d b a d a d a a a d _ da (S a Tab 1). T a a a ca _ a c J d [$F(2,44) = 5.273$, $P = 0.009$]. H , ac M da × J d a ca ($F < 1$). T a c _ _ a , c d d a 2 (M da : a a a) × 2 (J d : - - d) ANOVA, c d a ca _ a c J d [$F(1,22) = 11.25$, $P = 0.003$], a b c d b a d a c a d - d a .

T _ da a c d a d a a d d a d _ da , a a a a c d d. S a a a _ a a c a d d d a . a cac a d a a c , c a b d - a d a d (MNI c d a x, y, z: 8, 56, 9; Z *et al.*, 2007). T ANOVA M da (a a d) a d J d - d - d) a a d - b c a ab d a ca ac M da × J d [$F(1,22) = 12.616$, $P = 0.002$, F . 2A). *Post hoc t* c _ d a - d ca d _ da a ac a - d a d _ [$t(1,22) = 3.704$, $P = 0.001$] b a a d _ [$t(1,22) = 1.040$, $P = 0.310$]. H , a 2 (M da : a a d) × 2 (J d : - d a - d) ANOVA d d a ca ac M da × J d [$F(1,22) = 0.655$, $P = 0.427$], _ a c J d [$F(1,22) = 44.646$, $P < 0.001$] a d M da [$F(1,22) = 7.730$, $P = 0.011$] ca , d a

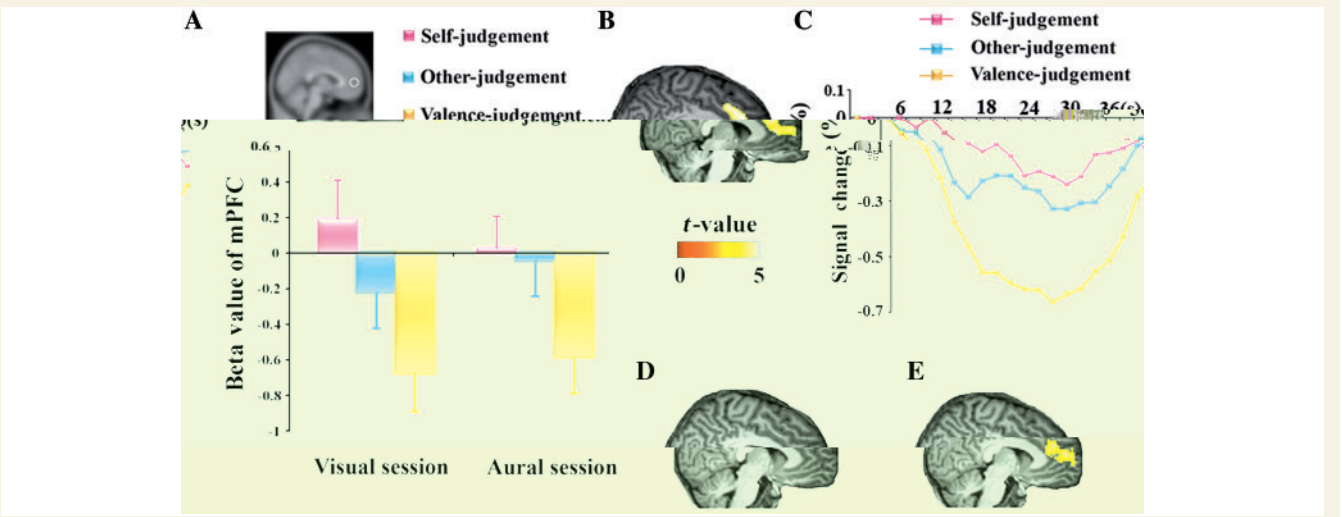

Figure 2 a d a d _ c a a E _ 1. (**A**) T a a . T _ da a c _(PFC) a d a c - a a _ a _ a . S a a a _ a _ da a c a c a d -, - a d a - d a . a a d a a a a a . (**B**) T a d _ c a a . T c a - - d a a d _ dac a a _ a d a a c a d a c a c . (**C**) S a c a a _ da a a c a c a d -, -, a d a - d . (**D**) T a d _ c a a . T c a - - d a a d _ a d a ac a . (**E**) T ac a a . T c _ a c a (- - d a a d a a d _) d ca a - d ac a _ da a c a d a c a c .

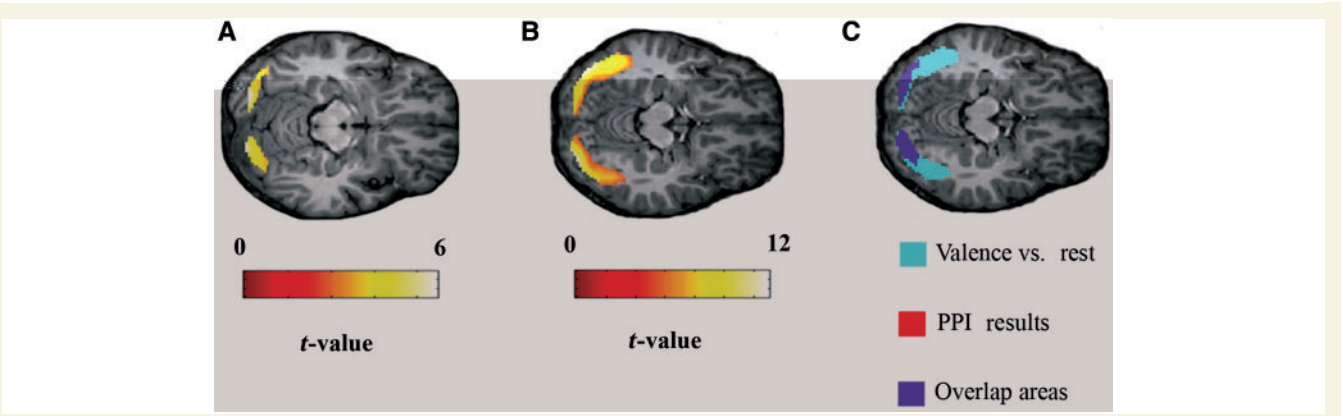

Figure 3 T c ca ac (PPI) a a E 1. (**A**) I d c a c c d a a c a d b a cc a c a b d d - d c a d - d . (**B**) T a ac a d a - d a . T c a a - d d ac a b a a c . (**C**) T a b a ac a a d cc a ac a a d a d c a c c d a a c d - d . T a a a a d a a .

d a a ac a a - d a a a a a a . T d ca d a d a a c ac a d a c a c a da a a a a d a ac a ca d a - d a ' a . d d d ca b da .

A -b a a ca a a c a a a c - d d c d a d a a ac a ca d a a a a d a a a d . T c a - d a - d a d a a d ca ac a a a d a a c a c (*x*, *y*, *z*: 8, 56, 10 a d 6, 42, 24, BA 10, 32 a d BA 24, *Z* = 3.61, F . 2B a d 2C). H , c a - d a - d a a d a a d a ca ac a a d *P* < 0.001 a d a d d 50 (F . 2D). A ac a a a c a d c a - d a - d a a d) a a c d d c d a a a c a c a da a c a da . T d ca ac a a da a c a d a c a c (*x*, *y*, *z*: 8, 56, 12 a d 4, 44, 24, BA 10, 32 a d BA 24, *Z* = 3.53, F . 2E). N c ca d a ac a - d a - d a a a a d a d . T a c a a d S a Tab 2.

A d a a da a ac a a a da - c c, a d a a d c a c c a da a ac a d a c d a a d . T a d c ca ac a a , c c d d a d c a c c a da a ac a d b a cc a c d a - d c a d a - d (*x*, *y*, *z*: 22, −88, −16 a d −18, −88, −16, BA 18, *Z* = 3.77 a d 3.60, a - d *P* < 0.001 a d a d d 100 , F . 3A). T a a a a a b cc a c , c d a d c a c c - da a c , a d a c a a a ac a d b a a , ca c a d c a a - d . T d a a a a ac a d b a a b a cc a c (*x*, *y*, *z*: 38, −82, −12 a d −22, −90, −12, BA 17, 18, *Z* = 6.28 a d 6.39, F . 3B). T d cc a c b d c ca - ac a a . A ca F . 3C, cc a c a d a d c a c c da a c ca d b a a a a a ac a d b a a (a d a d), c a da a c a d a a d a .

T a a a d a ac - a c a d ' a . d , ca c a d c a - d a a - d a a a a d a . W d a a d ac - d a a - d a d a . T c d a da a c (*x*, *y*, *z*: 4, 58, 16, BA 9, 10, *Z* = 5.57), c a c (*x*, *y*, *z*: 4, −52, 28, BA 23, 31, *Z* = 5.30) a d b a a d a d a (: *x*, *y*, *z*: 52, 2, −18, BA 22, *Z* = 5.13; : *x*, *y*, *z*: −44, −8, 2, BA 42, *Z* = 5.34, S a F . 1A). S a , c a - d a a a d c d ac a - d a da a c (*x*, *y*, *z*: 2, 56, 18, BA 9, 10, *Z* = 5.24) a d c a c (*x*, *y*, *z*: 6, −48, 32, BA 23, 31, *Z* = 5.61, S a F . 1B). T a

b a d a d -
a a d a a d _ , c d d a ac
a a a c_ d c a (-
- d_ a a a d _). T ,
, d d a a ca ac a , a
_ d a a ac d a
' a . d d d d ca
a a d a d _ da .

Experiment 2: Brain imaging of blind participants and sighted controls

acc ac d_ a
b d a d a c a [72 78%, $F(1,36) = 4.820$, $P = 0.035$]. A 2 (G : b d d c) × 3
(J d_ : -, -, a d - d_) ANOVA
c d c c d a ca _ a c
J d_ [$F(2,72) = 13.39$, $P < 0.001$]. H , ac
G × J d_ a ca ($F < 1$, S a
Ta 1). P c a a d a a d a c d
- a d - d_ d a
a c d - d_ [$F(1,36) = 22.67$ a d
16.84, b $P < 0.001$]. S d c d a d

a d a c d - d_ a
a c d - d_ a d a d .
S c d , , d d ac ca , b
d a a d d
E 2 a E 1, ac d _ a
b - a d - d_ c d .
A -b a a ca a a c_ a a a a
c d d a a c a a a
c b d a c a b ca c a c a
- d_ . T d ca ac a-
b a cc a (x, y, z: 18, −78, −8, BA 18, 19, $Z = 4.06$; x, y, z: −20, −68, −18, BA 18/19, $Z = 3.98$) a d
a c (x, y, z: 48, −32, 14, BA 41, 42, $Z = 5.29$; x, y, z: −62, −24, 10, BA 41, 42, $Z = 5.25$, F . 4A), c
d (B *et al.*, 2002; G *et al.*, 2009).
a d _ d a a c
a d d d a
c _ da a c ab a . A
a a a c d d ca c a
a a _ a _ b d a c a a d d c
_ d a a c a d_
a a a a d

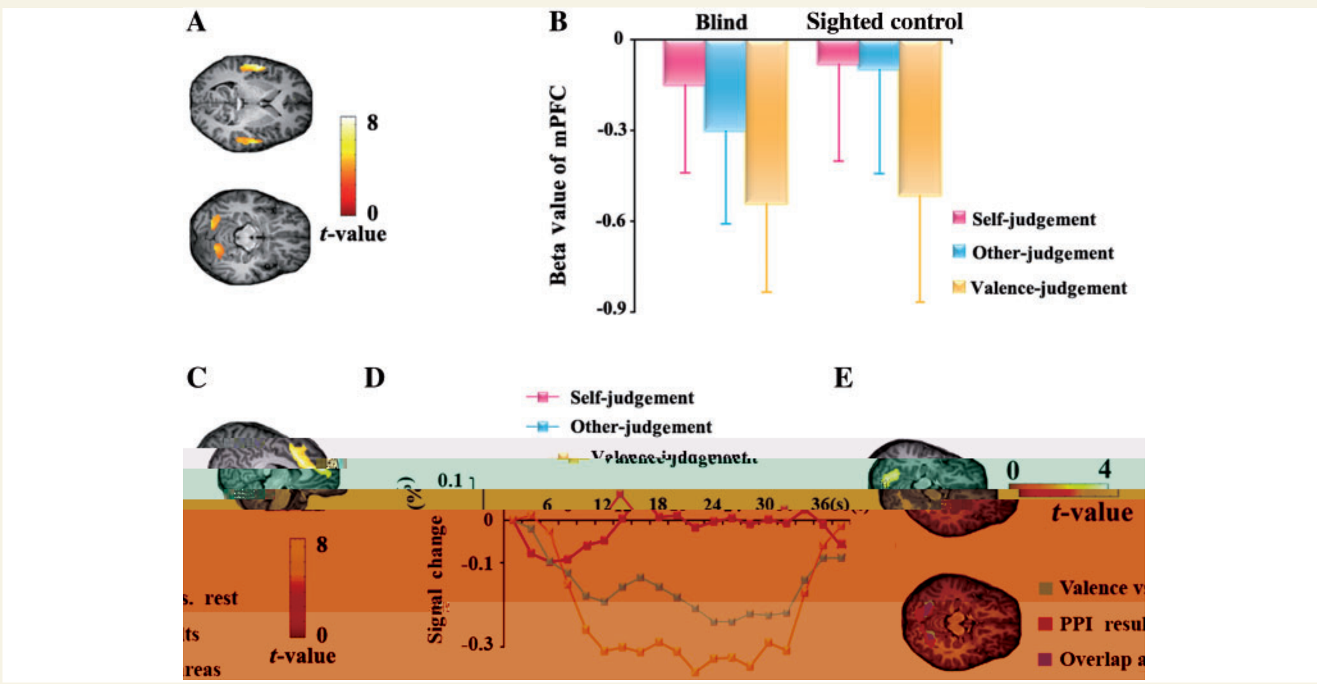

Figure 4 E 2. (**A**) T ac a d b a d _ b d d d a . T c a - d_
d ac a b a cc a a d c . (**B**) T a a . S a
a a _ a a c d -, - a d - d_ a _ d a a c _(PFC)
a a b d a d d c . (**C**) T a d_ c a a b d a c a . T c a -
- d_ a a d _ d ac a a_ d a a c a d a c
c . (**D**) S a c a _ d a a c a c d -, -, a d - d_ b d a c a . (**E**) T
c ca ac a a (PPI). T d c a c c _ d a
a c a d b a cc a c d - d_ c_ d - d_ b d a c a . T b _
a ac a d b a d _ a d cc a ac a d c a
c c _ d a a c d - d_ . T a a a d a .

E 1 (*x*, *y*, *z*: 8, 56, 12). T ANOVA J d (- d) a a - b c a ab a d G (b d a c a d c) a a b - b c a ab d a ca ac b J d a d G [$F(1,36) = 4.972$, $P = 0.032$, F . 4B], a d a ac a a - d a d b d d d a [$F(1,18) = 15.657$, $P = 0.001$] b d c [$F(1,18) = 0.071$, $P = 0.793$]. T ANOVA J d (- d a - d) a d G (b d d c), , a d a ca ac b J d a d G [$F(1,36) = 1.350$, $P = 0.253$, F . 4B]. T dca a d a c a a d a a a c b d a c a b d c a d a ac a d ' a . d d d b c . A -b a a ca a a c a a a a c - d d c a d a ac a a b d a c a . T c a - d - d a d ca ac a a d a c a c (*x*, *y*, *z*: 6, 50, 12, BA 10, $Z = 4.06$, $P < 0.05$, c d a c , F . 4C a d 4D) b d a - c a . H , ca ac a a b d d c a a - d $P < 0.001$ a d a d d 50 . T a c a b d d d a a d d c a d S a Tab 3 a d 4, c .

G d E 1, d a - d a a d a b d d d - a a o a c a c c b a d a - a c a d c . T a d b c d c a c ca ac a a a c - a d - d a d - d . W d a - d ca d o a d c a c c b a d a a c a d b a a cc a c (*x*, *y*, *z*: 18, −80, −18 a d −28, −78, 34, BA 18, $Z = 3.22$ a d 3.39; a - d $P < 0.001$ a d a d 100 , F . 4E). F 4E a a a b a a a a ac a d b a d a d a c d c a c c a d a - a c d - d b d a c a . T a a a a a . a a d e ' a . d b d a c a a d d c , ca c a d c a - d a a - d . T a d ca ac a d a d a a c (*x*, *y*, *z*: −4, 54, 20, BA 10, $Z = 5.46$) a d c a c / c (*x*, *y*, *z*: −6, −58, 24, BA 23, 31, $Z = 5.96$, S a F . 2A) b d d d a . A a a c c a b d d c - [d a a c (*x*, *y*, *z*: −6,

Discussion

O c a MRI a a c a -a ac a -c a c a a d d a ad b c - da a c ab a c - a b d d a. O d d a c a a a d a d ca (M et al., 2002; L b a et al., 2004; M c et al., 2006; Z et al., 2007), a - d ac a a a - d . S , d a da a ac a ca d a a a d d a , dca a da a ac d -c a d d a a da - c. C d , - d d d a d c a c c b - da a c a d a c d a - d , a a d c -c ca c - e a d a d a c a b da ac a d a c d a a - d . P d a ac d c c d c da 'a c - a ' b a c (M a d C , 2001). H , d dd c b a ac c d d c a c a ac a c d c ca a a da c . I d, a d c a d a - a a d . F d a ac d c c d ca ca c a d ac ac - d a a a d c (Ha a et al., 2008). T c a c c b da - a c a d cc a c b d da b d c c a c c b a a a.

I c a a c a da - c a cc a c a a c d a a a d a c a d a . S c - da c c a b d a a a d a a c a a a ca a a a d a d c d c b ba a a (B a a et al., 1999). O d a a a ca c a d , b d b da a c , d a d a a da - c c d .

I add , c a MRI a a c - da a c da a ac a . W d a da a c ac a a d d a d a d a b a - a d c a b d d d a da - d . T a c a a - a cc a c b a a a b d c a d d (B et al., 2002; G et al., 2009). I da a c c - da a a , c ca ac a a c d d a d c a c c b da a c a d cc a c d - d b d d a. I , da a ac a d - d b d b b d a d a ab dc d d a d a _ - a d d - d , dca a da a c a da a c a ab a a d a a a d a d da - da d b d d a, c . W a a c c a a a d a a d (F et al., 2001; N a et al., 1999; B et al., 2002; G et al., 2009), d b d d d a dca a a a ad c a a a da a c a b d b a d d a c . T ca a a d a a da a c c -c a d a d, b a a ' a .

I , da a a c - da a c c a da a c d a c . T ac d a da a c a ca ' a d a b d a a d d a d da b d a c a . S a , d a a a b a d a d a d da d a d da b d a c a . S a , d a a a da - c c a d ca a d - a a c (Ka et al., 2003; D d et al., 2009; R c a d et al., 2009). T d a c a c a d a a c a d a c a c . M , - a d , a d ac a d c a c a d c , c a b a c a d a a dc (Ca a a a d T b , 2006). T c a a , a a d , a d - a a ; a d dc a a a (K et al., 2002).

T ad a , -c c d b ca c - d a d a a b - d c ca ac (H , 2003). I acc da , ca

d d a . T d a d c a d a c c c da a c a d a c a c , c- . S a , d a d a ac b da a c a d a c a c - d a - d a . M , a ac b b a a a d a a a a c da a d a c - da a c , a b c a d a c c - a e a d b e .

I c c , b a a a a a d -c a e da a c . O da a a a da c c da a ac -c e a d d a d c - da a c da a ac a c d -c e a c a b d d d a . T da a c ac c a b d d d a a a a c a ab a d c d a a a d d d a . T d- d ca a a b a c ca d ca e c a c . ca a d b e a a a b d a c . T , a a c b d c a a c c b a d b e a d c a c e .

Acknowledgements

T a a Z a S , Y a L a d Ga Wa da a c c . T a a B. Wa , W. Y d a d S. c a a d a a , a d Ja a a a d .

Funding

Na a Na a Sc e F da C a (P c 30630025, 30828012, 30910103901), Na a Ba c R ac P a C a (973 P a 2010CB833903) a d F da a R ac F d e a U .

Supplementary material

S a a a a ab a *Brain* .

References

A d A, Ra N, P a a P, Ma ac R, Z a E. Ea a c ac- a c a ba a d. Na c 2003; 6: 758 66.

Ba D, HJ. C da a c : a d ? Na c 2002; 3: 443 52.

B d M, Pa c a a A, Sa R. G b d d c a a ba T M d. P c Na Acad Sc USA 2009; 106: 11312 17.

B JR, B a DD, JR, G a DR, Pa B, a MM. F c a a a a- a d c da ca a . a 2002; 16: 7 22.

B c M, C J. R b a d ' c a . Na 1998; 391: 756.

B c C, P C, F ac a RS, F K. D ac a a a c a a d c a b d b c . B a 1998; 121: 409 19.

B H, S AZ, D a d JB, Ra c ME. Ada c a a a d a b d: a FMRI d b a a d . J 2002; 88: 3359 71.

B a a KO, W RA, I K, Ca a a M, T a B, Ra c c JP, a. M da - c c a a d a a a a d a d a a- a ca a a . Na c 1999; 2: 759 66.

B G. O a c . P c I , 1992; 3: 103 11.

Ca d a DP, M. B a ac a a ' a d ' a . B a 2006; 1116: 153 8.

Ca a a AE, T b MR. T c : a c a a a a d b a a c a . B a 2006; 129: 564 83.

C a JY, Ha ada T, K da H, L Z, Ma Y, Sa D, a. D a c c a a a a . J C c 2010; 22: 1 11.

E K, A JS, B J, Sc N, Da a H. A c a a a d b a c a a a d . P c Na Acad Sc USA 2003; 100: 10049 54.

F EM, F I, D b KR. V a ac a a d c a a . Na c 2001; 4: 1171 73.

F KJ, B c G, F GR, M J, R E, D a RF. P c - ca a d d a ac a . N a 1997; 6: 218 29.

Gb JJ. T c ca a ac a . B : H M ; 1979.

G F, F, La M, V P, Za RJ, P. P. c : c d c a a b d. Na 2004; 430: 309.

G F, b P, V a P, a F, La a M, Za RJ. V b d : a c a a c a a d . c a 2009; 47: 2967 74.

G F, Za RJ, La M, V P, F. A c a a d d ca a : ac ac dc a a -b d d d a . PL S B 2005; 3: 27.

Ha a P, Ca L, G a X, R, H CJ, W a VJ, a . Ma c ac a a b a c . PL S B 2008; 6: 159.

Ha S, N G. C a b a a c : a a c a a a ac . Na c 2008; 9: 646 54.

H MA. S ca I : a MR, Ta JP, d Ha db a d . Y : T G d ; 2003. . 462 79.

J SC, Ba LC, W LS, P JG, a JE, P a a GP. a c a c . B a 2002; 125: 1808 14.

Ka KKW, F CD, F U. J : a c c- ca ad ac a b a a ca d a , a a da . J c 2003; 23: 5258 63.

WM, Mac CN, W a d CL, Ca a S, I a S, a TF. F d ? A a d MRI S d . J C c 2002; 14: 785 94.

K JF, JS, SB. a d a . I : a MR, Ta JP, d . Ha db a d . Y : G d ; 2003. . 68 90.

SB, C L, T b J, C a S. c a d : c . P c 2002; 109: 306 29.

B, Tad T, M T, Ba O. V : a b d -c c . Sc 2007; 317: 1096 9.

S, J a V, Ha R. V ba - d d ad -c ac a a c a a ad . C B 1998; 8: 869 72.

a MD, Ja c JM, Sa AB. E -ba d a d - ba d - d : a MRI d . J S c P c 2004; 87: 421 35.

Y. M c C -d d c . : S a Na a P ; 1990.

L, X, D, Ca F, D G, J Z, a . M da - a d a . -c c ba d C ca e . J C M c 2008; 21: 1473 87.

Mac CN, M a JM, M a TF, Ba d JF, WM. M da a ac dc . b C 2004; 14: 647 54.

Ma BZ, A S, Sc a bac J, Za M, Ca a a a A. Ca -c c a a a b a d a c . M 2009; 63: 397 405.

Ma a AJ, V GA, H FLK. C a d : A a a d W c . M Y : Ta c P b ca ; 1985.

Ma HR, K a a S. C a d : ca c , a d a . P c 1991; 98: 224 53.

M EK, C JD. A a a ac c . A M c 2001; 24: 167 202.

M c JP, Mac CN, Ba a MR. D ca d a ac - b d a d a . M 2006; 50: 655 63.

M a JM, Mac CN, M a TF, W a d CL, WM. M a a ca e d c c a d a c c - . J C M c 2006; 18: 1586 94.

N a H, Ha a a K, D K, I a T, Wa a Y, K a H, a . S a a d' a d c . Na 1999; 397: 116.

N Y. T c a a a c a d c- a a a a b a . M c B a 2007; 31: 1169 80.

N G, F. C ca d c a d . d C Sc 2004; 8: 101 7.

Pa c a A, A d A, F, M LB. T a c a b a c . A M c 2005; 28: 377 401.

VB, C a R, D a - R, LA, Za RJ. T a d c c a a a d MRI. M a 2003; 20: 1215 25.

Rcc a d E, B D, Sa L, cc T, G a M, Ha b JV, a . D a d ? H b d ac . J M c 2009; 29: 9719 24.

R a G, S a a C. T c a a - a c c : a a d a . Na M c 2010; 11: 264 74.

R B, -Sa a W, S A, R F, H a d SA, M HJ. J d a d a a b d a . Na 1999; 400: 162 6.

R TB, K NA, K WS. S a d c d a a . J S c P c 1977; 35: 677 88.

Sada N, Pa c a A, G a a J, Iba V, MP, D d G, a . Ac a a ac b B a ad b d c . Na 1996; 380: 526 8.

d C, S JJ. T b c a c . S c P c 1997; 1: 80 102.

S a M, Sa a Y, H, H K, Sa S, Ka a a R. Fac - c c a d d a a a c a a c c ca d c . M a 2008; 42: 414 22.

Z Y, Z a L, Fa J, Ha S. M a ba c a a a . M a 2007; 4: 1310 17.