Behavioral/Cognitive

Perceptual Learning at a Conceptual Level

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Humans can learn to abstract and conceptualize the shared visual features defining an object category in object learning. Therefore, learning is generalizable to transformations of familiar objects and even to new objects that differ in other physical properties. In contrast, visual perceptual learning (VPL), improvement in discriminating fine differences of a basic visual feature through training, is commonly regarded as specific and low-level learning because the improvement often disappears when the trained stimulus is simply relocated or rotated in the visual field. Such location and orientation specificity is taken as evidence for neural plasticity in primary visual cortex (V1) or improved readout of V1 signals. However, new training methods have shown complete VPL transfer across stimulus locations and orientations, suggesting the involvement of high-level cognitive processes. Here we report that VPL bears similar properties of object learning. Specifically, we found that orientation discrimination learning is completely transferrable between luminance gratings initially encoded in V1 and bilaterally symmetric dot patterns encoded in higher visual cortex. Similarly, motion direction discrimination learning is transferable between first- and second-order motion signals. These results suggest that VPL can take place at a conceptual level and generalize to stimuli with different physical properties. Our findings thus reconcile perceptual and object learning into a unified framework.

Key words: perceptual learning; motion direction; orientation; transfer

S ca c S a

Training in object recognition can produce a learning effect that is applicable to new viewing conditions or even to new objects with different physical properties. However, perceptual learning has long been regarded as a low-level form of learning because of its specificity to the trained stimulus conditions. Here we demonstrate with new training tactics that visual perceptual learning is completely transferrable between distinct physical stimuli. This finding indicates that perceptual learning also operates at a conceptual level in a stimulus-invariant manner.

I d c

O f a a f f a a a a f a a a . S f f a a , a a a U a f , a a a f f a f a f a (B a ., 1956; R a Ra ff, 2006). A a , a ff a a U a a a f a a a a a ff a . S a a a f a a f a . C , a a a (VPL) - a ff a a f a a a f a f a a a a a a f a f a (Fa , 2002). F a , a (. ., - a ff) f a ' a - a , a ff a a a a a a a a f a a / a 90 (C a ., 1997). S a f a a a (V1), ff ff a f -

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a , a , a (H a W , 1959, 1962). T , VPL a a - a V1 a (Ka a Sa , 1991; S a ., 1995; T a Q a , 2003), a a V1 a a a a a (M a Da a, 1996; D a L , 1999; La a G , 2009).

H , a a a a a / VPL a a - a a - - (TPE) - (X a a ., 2008; J.Y. Z a a ., 2010; Z a a Ya , 2014; X a ., 2016) a a a a a a a (Wa a ., 2012). F a , V a a a a a a a a a a a a a a (Wa a ., 2012, 2014; J.Y. Z a a ., 2014). T a a - a a a a a a a a a a a a a a a a a a a a a a a a . I a , a a a a a VPL.

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Observers and apparatus. S - a (33 a a 41 a) a - - a a a a a a . A a - (F . 5G) . T a . A a D a a H a a B N a U a P U .

T a a MATLAB- a P -3 (P , 1997) a a 21 S G520 (1024 × 768 , 0.38 × 0.38 , 120 H a a). T a a a 50 / 2. T a a - a U a 8- - a . V a a a - a (a = 17) a a a a a . A -a - a a U a . E a . A E II a (SR R a) a a (F . 5F).

Visual stimuli. T a a a Ga a a a a a a a (F . 1A). T Ga a (Ga a - a a) a 1.5 / a 50% a , a a U a . T SD Ga a a 0.67 . T a (S a ., 1995) a a a (3 a). T a a a a 0.09 a 0.37 a - a U a a .

T a 18 a a a - (0.1 a), a a a 18 × 18 a a (0.16 × 0.16 a). T a 18 a (18 9 a a a a) a a : (1) a a a a - a ; (2) 8 , 2 a 3 a a a a - 6 a 2 ; (3) a a a 18 a a 18 a ; a (4) a a a a - 0 0.04 a . A - 18 a , a a a a a 18 - a . F a a , a a - a , a a a .

T a a a - a (. ., -) a a - a (. ., -) a a a - (P a Ha , 2010). I , a - a a a a a a a a a a , a a - a a a a a a a . T - a a a a 6.5 , a 1, a 4 / . T a a a a a a a 5.5 6.5 a .

Experimental procedure. I a , , - a , a a a a , a a a 2-a a - a a 3- 1- a - a a a a 79.4% a .

I a a , a a a (a a a : 106 a ; a a : 800) a a a a (a a : 500 ; a : 200). F a a a a , a a 35 125 a a a a a a a a a a . T - , a a a a . F a a a a a , a a a a U ±20% a a a . T a a a a a a a a a 80% a a a . T a a a , a , a a a a . T - , a a a a a a a a . F a a a - , a a 1.00, a a a a a a a a . T ' a a a a a a .

A a a . Ea a a 10 a (~50 60 a). T a a a a a a a a . T a a a a a a a a . T a a a (a) a a a 16 10 a a , a a .

I a a a a (F . 5G), - a a a 1 a a a a a 5 a a . I a 4 a a a . A a 200 a , a a a - - 1.5 , a a a a a a a a a a a . T - a a . A a a a a a a . T a a a a a a a a a . T a a a . Ea 48 a . T a (PSE) a 50% a a a a

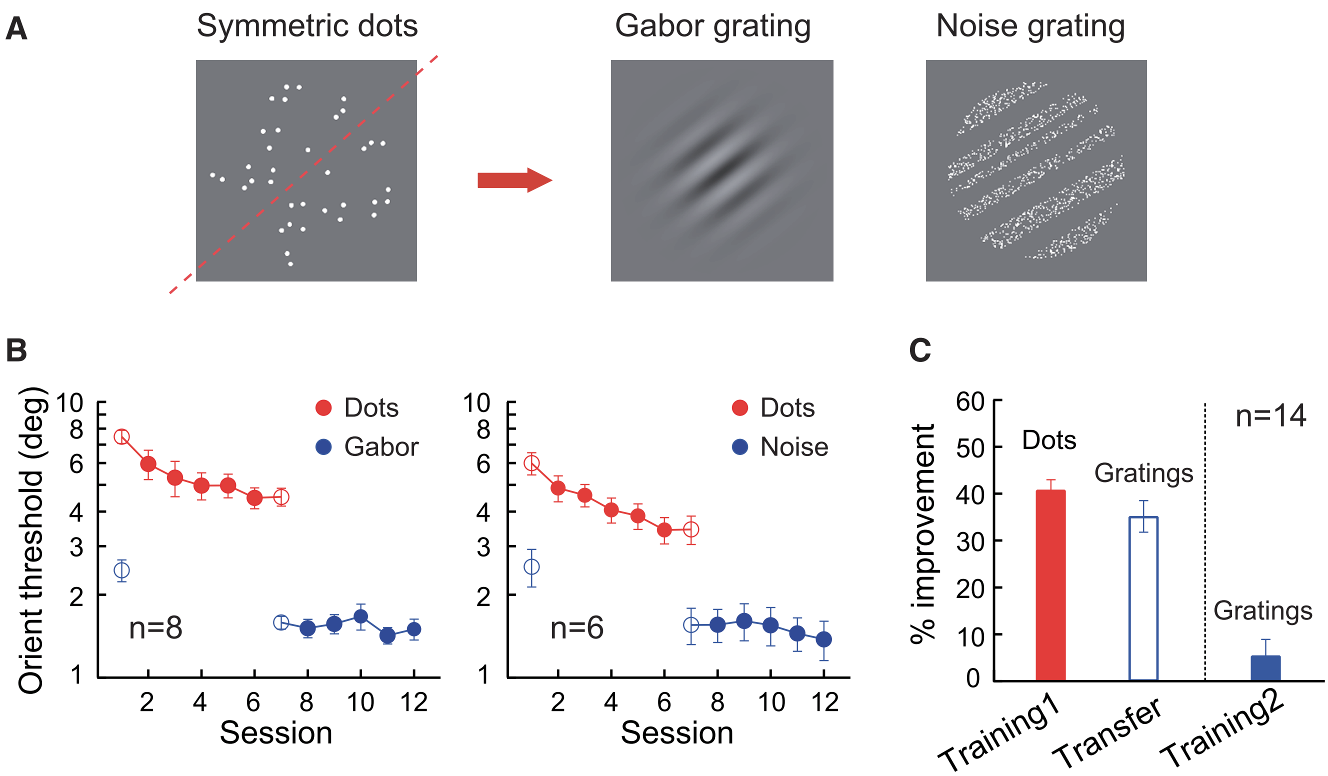

Figure 1. Transfer of orientation discrimination learning from symmetric dot patterns to gratings. ***A***, Sample stimuli. The symmetry axis is indicated by the red dashed line (not shown in the actual stimuli). The arrow indicates the direction of learning transfer. ***B***, Session-by-session mean discrimination thresholds for dot pattern orientation ("Dots") and grating orientation ("Gabor" or "Noise"). Grating orientation discrimination was tested with Gabor gratings (left) and noise gratings (right). ***C***, Summary of dot pattern orientation learning and its transfer to grating orientation ("Training1" and "Transfer"; left two bars) and the impact of further grating orientation training ("Training2"; right bar). Data are averaged over the two panels in ***B***. The percentage improvement was calculated as (pretraining threshold − posttraining threshold)/pretraining threshold. Error bars indicate ±SEM.

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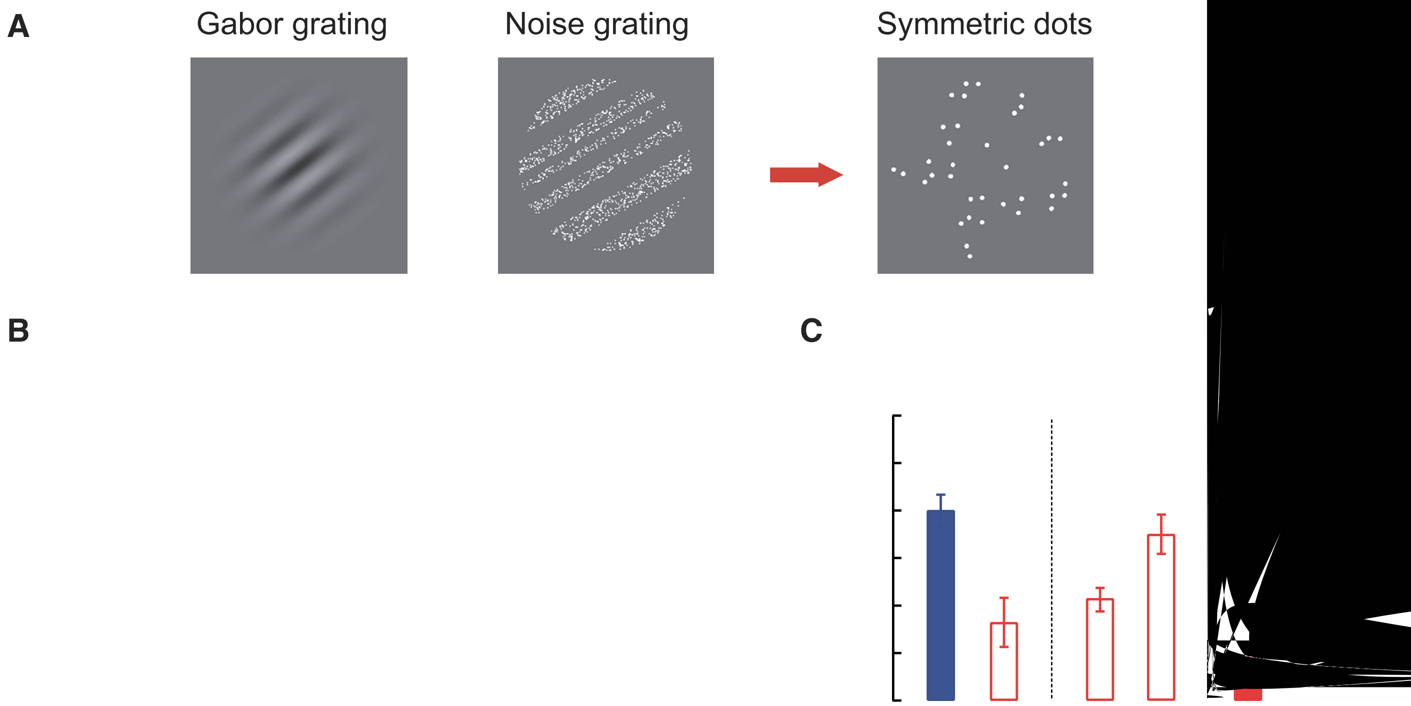

3.3% ($p < 0.001$, C ’ $d = 3.24$; F . 2B,C). T a
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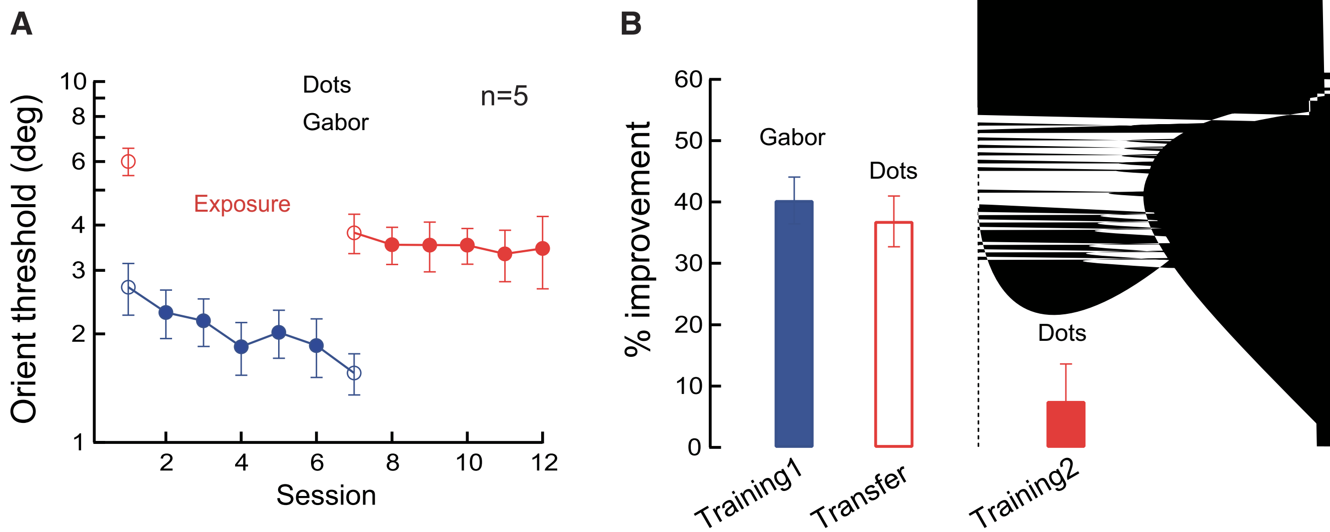


Figure 3. Transfer of orientation discrimination learning from gratings to dots patterns in a simultaneous TPE procedure. ***A***, Session-by-session thresholds, first with Gabor orientation training alternated with exposure of dot patterns and then with dot pattern orientation training. ***B***, Summary of grating orientation learning and its transfer to dot patterns ("Training1" and "Transfer"; left two bars) and the impact of further global pattern orientation learning ("Training2"; right bar). Error bars indicate ±SEM.

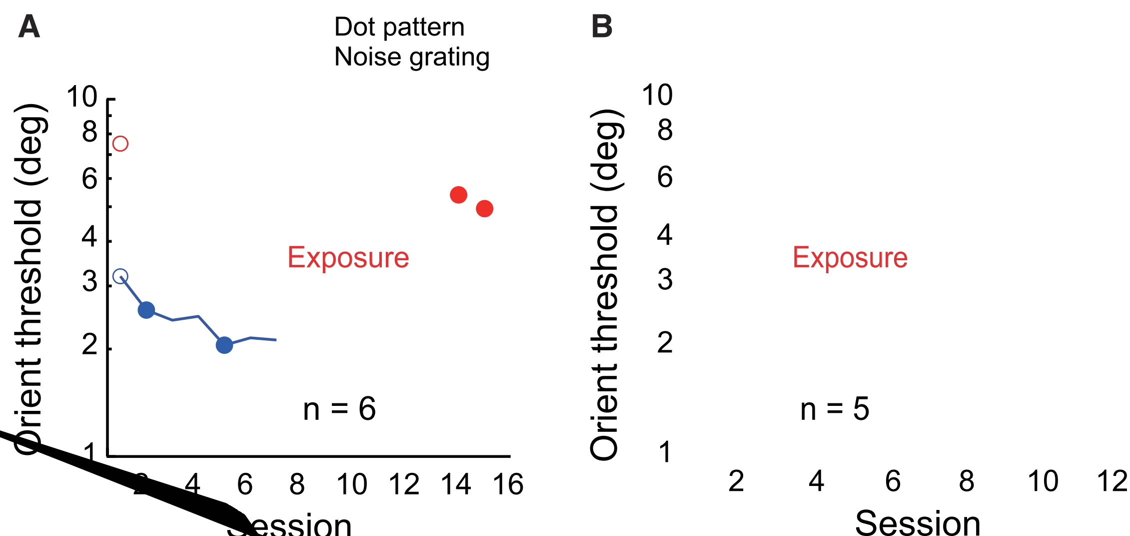
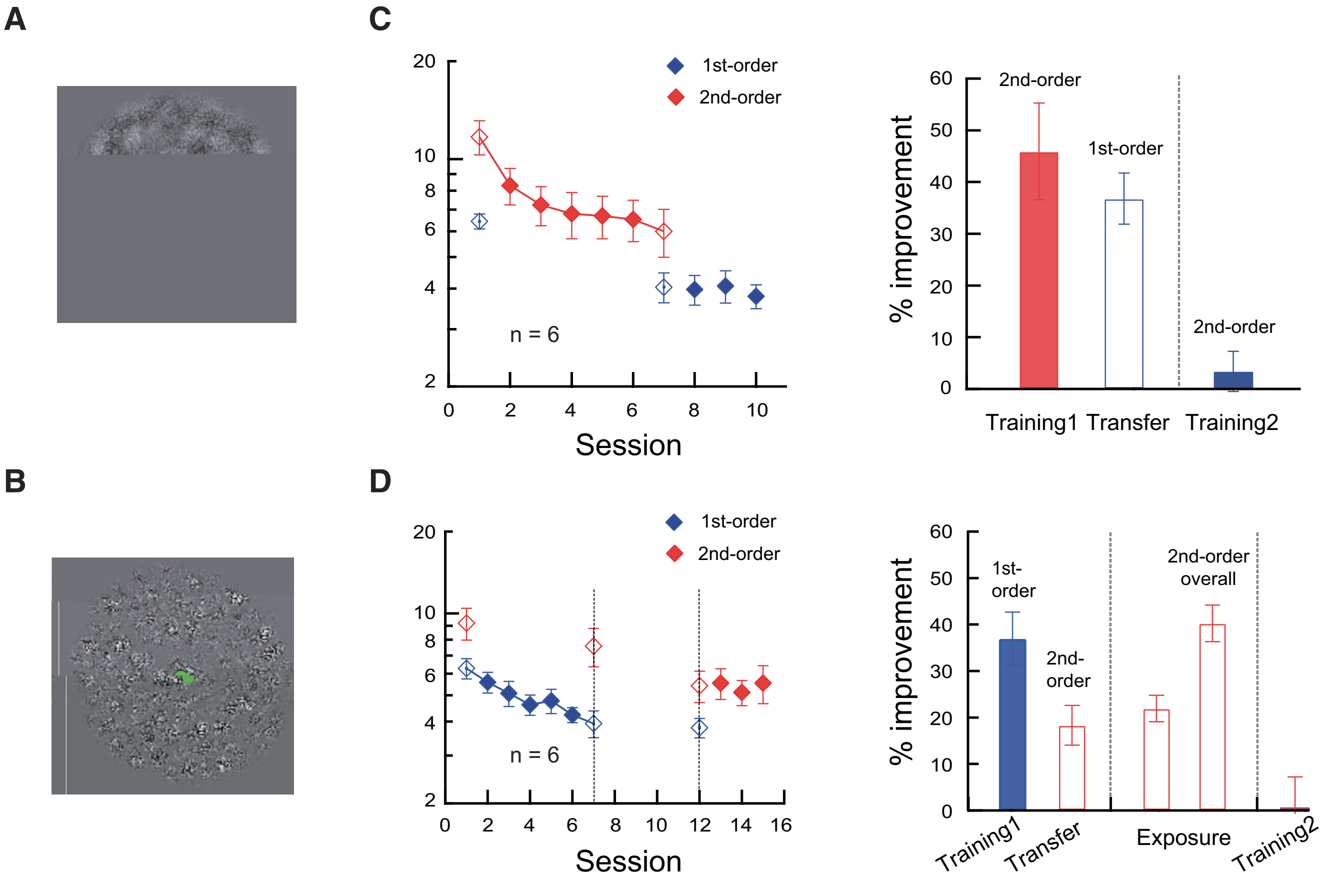


Figure 4. Two control experiments. ***A***, TPE enabled learning transfer from grating orientation to dot pattern orientation with a near-threshold exposure task. The experimental design was similar to Figure 2*B* except that the exposure task (sessions 8–12) was a near-threshold mean luminance discrimination task. ***B***, Effect of dot pattern exposure alone. The experimental design was similar to that in ***A*** except that there was no initial grating orientation training. Error bars indicate ±SEM.

(Ma a a M ; F . 4*A*). I a a a a (34.0 ± 5.1%, p = 0.001, C ’ d = 2.724) a a a a f a a a a a (9.7 ± 7.0%, p = 0.22, C ’ d = 0.57), a a - a a a (26.3 ± 4.5%, p = 0.002, C ’ d = 2.37). T TPE a U a a f a a a f - (−0.3 ± 5.8%, p = 0.96, C ’ d = 0.02). T a a a f a- a a .

W a TPE a a a f f a a , a a a a a a a a - . A . T

a a a a F 4*A* a a a a a a . A F 4*B*, f a (a a a a - a a a a) a a a a f a a a a (8.6 ± 4.5%, p = 0.115, C ’ d = 0.778), f a a a f a a - a a (24.4 ± 7.3%, p = 0.029, C ’ d = 1.49). C a f f a a , a a a a - a a a a a ff a a . T f , f a a a f a af TPE a a a a a a a , a a a a - a a .



T a a ƒ a a ƒ a - (L a S , 2001; A a a ., 2007). Aƒ 5 ƒ a a . T a - a (16 ƒ a) - a (ƒ -) a (F . 5A) a , 6 a ƒ a a ƒ a a - a (-) - - 45.9 ± 9.3% (p = 0.004, C ' a (F . 5B) a a a d = 2.0; F . 5C), a a ƒ a a ƒ f - (36.8 ± 4.9%, $p = 0.001$, C ' $d = 3.0$). A f 3 f a f - a a (5.3 ± 3.7%, $p = 0.22$, C ' $d = 0.58$), a - a a a f f - . S a a f f a a a f a a , - a a f - (36.9 ± 5.7%, $p = 0.001$, C ' $d = 2.6$; F . 5*D*) 6 a a a a f - a a (18.3 ± 4.3%, $p = 0.008$, C ' $d = 1.76$). T a a a f f - a - a a (P a Ha , 2010). N , af a - a a - a a a (Ma a a M) f 5 (16 f 50 60 a), a f a - a f 22.0 ± 2.9% ($p < 0.001$, C ' $d = 3.1$), a a f 40.3 ± 4.0%. T f a - f (−0.2 ± 6.0%, $p = 0.75$, C ' $d = −0.15$), a a a a a a f f f - - .

A a 5 a a f (a a f - f 5 ; F . 5*E*) a f a a (−1.1 ± 2.5%, $p = 0.45$, C ' $d = −0.20$). T a f - f a a a f a - af - a a a f - a a a - ; a , a a a a f - a a a .

A a a a f f - a - a a a a - a aa a . S a a f f a f . F a f - a a f a a a (f a a a). W a a , f a , a a a a a a . N a a a a a (F . 5*F*). T a a a a a a a Ba a S (1982) a a f fa a .

A f - a - a a a a . F a a f f f a a - a f a a a ff f f - - (F . 5*G*). T a - a a a f a PSE (. .,) f a - 24.2 ± 6.2% ($p = 0.036$, C ' $d = 1.82$). T a a a a a PSE f f - (4.3 ± 3.7%, $p = 0.034$, C ' $d = 0.59$) f - a a a f f - a a a - TPE (F . 5*C*). T a f - a - a a a a a a , a a a a a (A a a ., 2007).

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I , f a a f f a a a f f- f a a a ff a . I a a , fMRI (Sa a a ., 2005; T a ., 2005) a a - a a a , a a a a (LO), a ff a a a a a a , a a a- V1 a a . T a a a a - a LO a a f (Ca a a ., 2011; B a a ., 2014; B a a ., 2015). M , fMRI a a a a a a a a a f f - a - a (La a ., 2006) a (A a a ., 2007) a -a a a f a a a a f - a - . I F 5*G*, a a a a - a - a ff a ff - a - , a a a a a a a . P VPL a a a a f - a a a f a a (V a O a , 1987) a - a f f - a - (P a Ha , 2010; Va a a C , 2012

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