Perceptual grouping-dependent lightness processing in human early visual cortex

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Lightness, the perceived relative achromatic reflectance of a surface, depends strongly on the context within which the surface is viewed. Modest changes in the two-dimensional configuration or three-dimensional scene geometry may lead to profound variations in lightness even though the surface luminance remains constant. Despite recent progress, we are far from a complete understanding of how various aspects of spatial context affect lightness processing in the cortex. Here we use a novel stimulus to show that perceptual grouping through occluders can affect lightness. We first report behavioral results showing how lightness across occlusion depends on spatially distant image features, including luminance and contrast. Next using functional magnetic resonance imaging (fMRI) we show that human early visual cortex responds strongly to occlusion-dependent lightness variations with little or no attention. These results suggest that elements of three-dimensional scene interpretation play a role in early cortical processing of lightness.

Keywords: lightness/brightness perception, visual cortex, perceptual organization

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Introduction

T a f a F 1a a a , a a a f a . T f f a a w a a . Tw a a f a a a , a a w a a , f w a , a w a a a . T a a a , a a a a a wa w a w a a a (F 1a). I a , a a a a a . H w , a a F 1a a a , a w a f a a . I , a : a a a a a a a a a a f a a a a a (a a). H w w a a a a a , a a f a a F 1a, a a , a . T a w a a a a a a f a f a . T f a w a a a a wa - w a a a a a (Na a a a, S , & Ra a a a , 1990).

I f a a a , a a a a a w a a f a , w - a (2D) a a a a (A & S a , 1993; La & M Ca , 1971; L , 1999; M & K , 1991; O'B , 1958), a - a (3D) a a a a a (A , 1993; A & W aw , 2005; B , K , & H a , 1999; B a , D , S , & Ma , 2006; B a , Ma , & H , 2003; D , B a , & Ma , 2007, G , 1977; H a &

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B , 1954; K a a , K , & Ma , 2008; K & K , 1991; P a & M a , 2009; P , S , & L , 1999; R a a ., 2004) a a a a a aff f a f a . C - ff a a w 3D a -awa , a a (B a ., 2004; B a a ., 2003; S & B a a , 1996), a (G a ., 1999), a aa (K , Ma a a , & Y , 2004; P a ., 1999), 2D a a f a , a (B a & M C , 1999; M & K , 1991), a (La & M Ca , 1971; R & Z a , 2005; S a & R , 1985), a a (K a & Za , 2002). H w , a , a a a a a a w a f a. T a a a f a a w .

The role of early visual cortical areas in lightness processing

T a a a f a a a a . S a , w a a a a , a f -

a a a a a a (A , Da , & R , 2009; B a , Fa , M a , & K , 2007; Ha , L , & R , 2004; P a & M a , 2008; R , R , & Pa a , 1996; Sa a & Wa a a , 2004

ff a , w a a w ff a a a . H w w f - a a a f a a a .

Behavioral measure of the lightness effect in 3D stereo

Methods

Participants

T , w a FF a HB, a a . A w a a awa f f . A w - a , a - - a , a a w a a a . I f w wa a a a w a a H a S R w C f U f M a.

Display system

T - a w a - a a W a a w a . T wa f a S GDMC520 CRT a w a f a f f , . T w ff a f a af f a a - 3D . O w a 63.5 awa f a a w a a a . T wa a A Ma (P w Ma G5). C - a w a af a f a a f a a a w a (CAL, Ca R a S). T a w f a . T a - a a a wa 97 a a a (/ ^{2}; C I a a 'E a a [CIE]: x = 0.312, y = 0.339; a wa a a a a a . T wa a a f). E a f wa wa w Ja a a a a .

Stimuli

T w 3D a a (F 2a). T a a f a 12 6.25 f a a , a a w 0.625 7.5 (w ×). T a w a 1.9 a a f a . T a w a a a a f a a a a a a f 0.57 . A a - f a w a a a a a a f . T a a a a - , a ,

$$L = \begin{cases} L_a & \text{a f a ,} \\ L_a \pm L_a \times C & \text{a ,} \end{cases} \quad (1)$$

w C a , a L_a wa a af a a a a a . E a a w (0 1 w f 0.1). T a f a a a a a a . T a a , w a a a a a (0 255) a a w a 6 6 f , ff a a .

Experimental procedure and the task

T a a ' a wa a a f a a a a a (1° × 1°) a f a a a f a (F 2a). Pa a 5 a f a a a ; a wa a . T wa . T a f ff (*LE*) wa a a a w a a a a (- f a f a) a f w :

$$LE = \frac{L_a - L_a}{2L_a} \quad (C), \quad (2)$$

w (·) f .

Results

I a a a , w a a - a a f ff a af f a f a a (F 2). I a a a w F 2 . C w a a F 1a, ff w a f a a , a a w a a a a a . A , w a a a w f a a a : A w a , aa a a a a a a a a a a f a a a a a f a f f a , w a

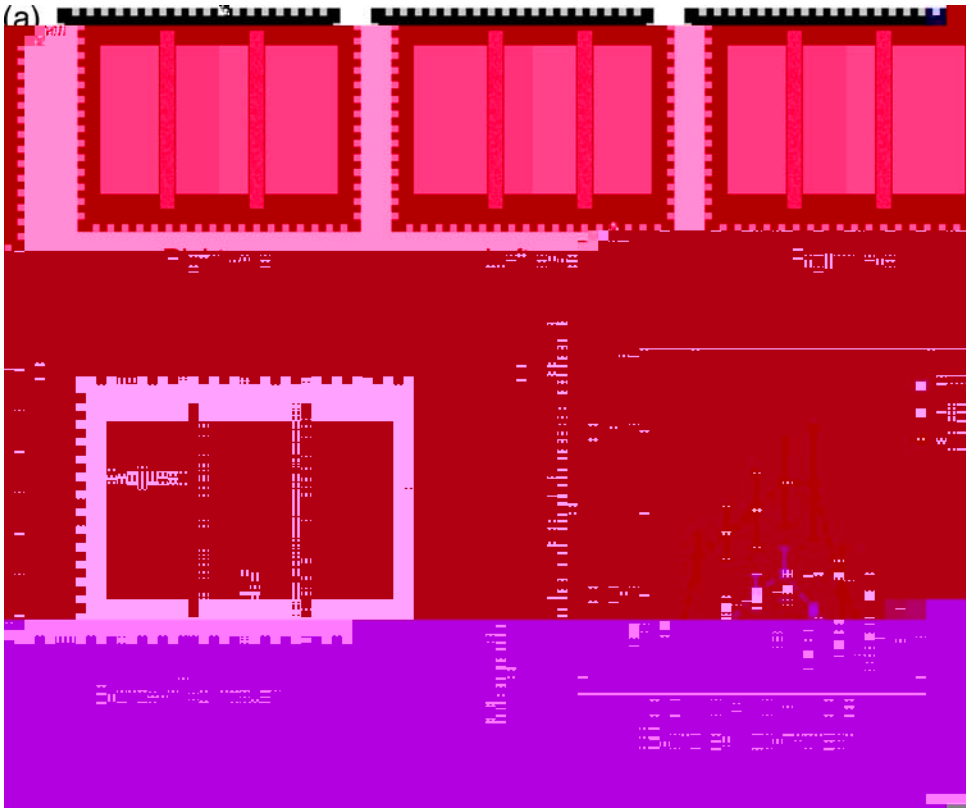

Figure 2. Behavioral measure of the lightness effect. (a) Stereo image pairs. Left pair for crossed fusion, right one for uncrossed fusion. (b) Task. Observers adjusted the intensity of a patch superimposed on one flank to match the intensity of the opposite flank. Eleven border contrast levels were tested. (c) Individual observer results. Magnitude of the lightness effect (computed as described in the text) first increases with the border contrast but then starts to decrease after mid-levels and nearly diminishes at higher levels. This is consistent with the subjective observation in Figure 1. (Error bars indicate 95% confidence intervals.)

ff . H w , a ff w a a a a a , aa a a f fa a a a a a fa , ff a . N a , a f a a a ff w a a a aa a , a a ff . H w , w a a a f .

Behavioral measure of the dynamic lightness effect in 2D

I f MRI w, w a f . F , f MRI w 2D. S , w a w a a w a a a a f . T wa a f MRI a a a w. B a f a a , aa a w a a ff a f MRI , w f a a a a 2D a a .

Methods

Participants

Tw , HB a KD, w a a a a a . I f w wa a a f a a a w a a a H a S R w C f U f M a.

Display system

T a a a wa , a wa a w a w a a a . O a a wa a f .

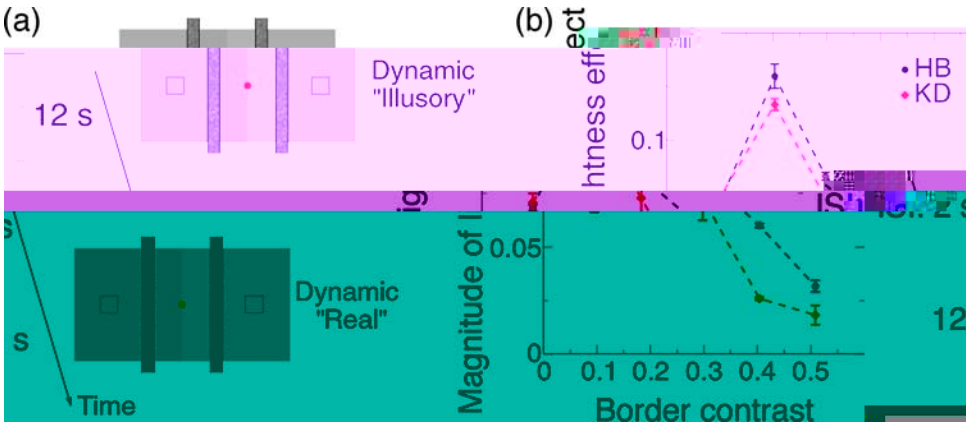

Figure 3. Behavioral measure of dynamic lightness effect in 2D. (a) Experimental design. In a 2IFC experiment, we compared context-dependent lightness changes to real luminance variations. Participants' task was to indicate the interval in which the flanks appeared to vary most during the dynamic display. (b) Results. Contrast of the perceptually equivalent real stimulus was estimated from observers' data and defined as the magnitude of the lightness effect. (Error bars indicate 95% confidence interval.)

Stimuli

Tw ff f w (F 3a). T I wa a a a a a (E a 1). T R a wa a , a a a a ff a : a f a a wa a a f a a . T a a f a 24 f a a . T a w 1.25 15 a w a 3.8 a a f a . A a a wa a f a a . Tw w f a (1.6° × 1.6°) w a f a a a a a , .

Experimental procedure and the task

A a a - a a (1- , 1- w) wa a w - a f - (2IFC) . I a a , a a -wa - a wa . T a wa 0.16 H , a a a f 4f a w a a (3- f a a). D , a a a . I a , a a a a a a . I a , a a wa w a a f 12 w a a (ISI) f 2 . I a , f wa . O w a a a a a a , w w f a , a a a a . B a f wa a a . Da a w f 5 ff a w a . Tw a a a w w a f a (20). T a f a a wa a w a a (W a & H , 2001) a a a f ff .

Results

T a w F 3a. C w , ff a , a w a . H w , a 2D , ff a a a w a a a 3D . T a a ff (f a w - a f -) a a a ff w 3D a 2D , w a a a , .

FMRI measure of the lightness effect

Methods

Participants

T a w a a a a a a a f MRI . I f w wa a f a a a a w a a H a S R w C f U f M a.

MR data acquisition

S a wa f a 3 T a a (S T) w a - a a -a a a . BOLD

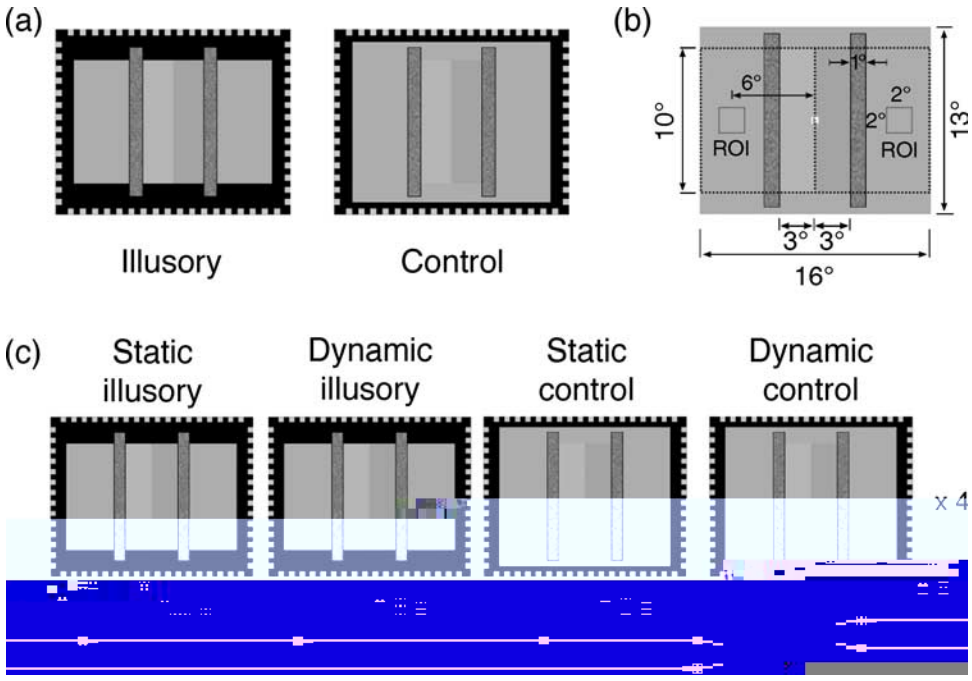

Figure 4. FMRI measure of the lightness effect. (a) Stimuli used in the experiment. The stimuli in the illusory and control conditions were identical except that in the control condition we added gray bands with the mean luminance below and above the occluded rectangular surface. While a strong lightness effect is observed in the illusory condition, the effect is nearly abolished in the control condition. (b) ROI definition. The experimental data were analyzed in retinotopically identified voxels that respond to the center of the flanks as marked by the small squares subtitled "ROI". (c) FMRI design. Both illusory and control stimuli were presented statically and dynamically in a block design. Average of last two time points of static intervals served as a common baseline in a scan. During the scan, observers performed a demanding fixation task to control for attention.

a w a w a - a a a (EPI) ([TE], 30 ; [TR], 2000 ; f w [FOV], 220 ; a , 64 × 64; a , 75 ; , 3 ; f , 28; a , a a). T f w a a w f a a . A - T1-w a a a - a (3D MPRAGE; 1 × 1 × 1 ^{3}) wa a f a a a a f f a a . Ea a a w f MRI ff a . O wa a a f w E , G , a Wa (1997) a S a . (1995). T a a a a , f (ROI) a a a , a f a f a f a ff .

MR display system

I a , w a - a (Sa P -X a PLC-XP41, f a 60 H) a a a . O w a a a . C - a w a f a f a f a a f a a f a a w a M a CS-100 C a . T a a a a wa 2917 / ^{2} (CIE: x = 0.314, y = 0.392).

Stimuli

T a a w F 4a a 4 . T a wa a a 2D. T - , w w a w f a I a C (F 4). T w a a a a - a - a (E a 1). T ff w a wa a f w a a w a a , L_a , a a w a a f a . T a ff a a f ff . I , w a a a a a a w. D a a , a a a . T f a a a . B a a f a , w a

a a a a a a a a a . I , a w a , w a a a a a a a a . Ba f a a a , a - a (. ., a a), w a f 0.25 f a , a ff w a a . *L* a wa af f a a f a .

Experimental procedure and the fixation task

I , w w w w F 4a. Ea wa a a f 18 a f fMRI a a , f w a 12- a -wa - a a a a 0.25 H . (F 4). A a a wa a a fMRI a . B a a a a f a f a a a a a (Ha a ., 2004), w a a a w - a a a a a . B f a , a a , a a a a a . Ea wa a 4 a a . A a 250 , a 10- a a a . T f a , a f a a a a a . T a a a a a a- f (100 150 f a , a : X a : Z , L , P , a J). O , a f a wa 61.46% (*SEM* 1.51) a a a a wa 606.52 (*SEM* 8.78).

ROI localization

W f (ROI) a a a a -wa - a a - (8 H) a a -a -w , a a a f 2 2 a , a a a w a a a a a . T ROI w a a 6 f a f a a . T a w a a f a a (F 4a). ROI a w f 12 f w a 12- a a , a f 7 . O a a wa f a a .

Data processing and analysis

U B a V a QX (B a I a , Maa , T N a), w f a a f 3D a a a a w a a a (a w 0.015 H ; S a ., 1999). T a a a a a w a f a a w B a V a QX. F a a , f a a f a a a w a a a f a a a w a a a a a a . B a- a w a a w aw a a w B a V a QX a f a a f - a a f BOLD a a w a f BOLD a a a (E a ., 1997; S a ., 1995). A a a (GLM) wa f ROI a a ($p(\ .) < 10^{-4}$) w B a V a QX a a a f a a a . T ff fMRI a a a f a ROI w a a f a a a w a Ja a af . T a a a - a a a f a (w a a f a w a f a a —a a a a a a a f a a a). W f a a BOLD f (a w 6 a 12) af f - a f a a a a *t*- a a a f ff a w - a a a a .

Results

Possible outcomes

T a a f a a F 5a. I a , a a a a a w ROI . T f , w a a a (F 5a). T w f - . H w , a w F 5 , a a a a a a f a a a a a fMRI a (C a ., 2006). T a a a a f a a a f a a , a a a a , a a a a w a a a a (F 5). B a a a a f a w a a a , w a a a w . T w a f - , a w . N a wa - a f a a wa a a - . T a wa a a a a a a

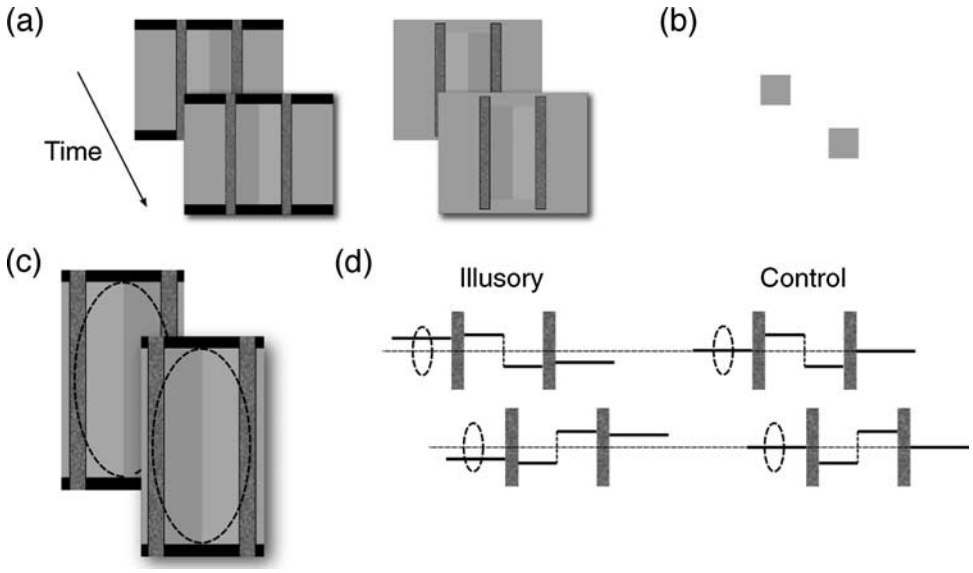

Figure 5. Possible outcomes of the fMRI experiment. (a) Dynamical presentation of the stimulus. (b) Because there is no physical change at the flanks, in the null hypothesis we expect no increase in fMRI signal to dynamically presented stimuli. (c) Alternatively, because of distant physical changes we would expect an increased fMRI activity. If these temporal physical variations were the sole factors driving the activity in the cortex, we would expect the fMRI signal to be identical across the illusory and control conditions. (d) Lightness changes at the flanks only in the illusory condition, not in the control condition. If the cortical activity correlates with perceived lightness rather than physical luminance, we would expect to find a larger fMRI activity in the illusory condition.

w a a a a w a a . I , a a a a w a a a . T a ff fMRI a w w . H w , ff f f a a a a f a a a a ROI . A a a a , w a a fMRI a , a a f a a a a a . f a a , w a f - a a a a . T f fMRI a w F 6. T f fMRI a a a a a a f V1, V2, a V3 a F 6a. F 6a w a a f , w w a a a f a f 3 6 (6 12). T a a a wa a a f a a a w a ($p < 0.001$). T f , w a w a a w - a , w a . N a a a a a . T a a a f a ff (w a a a a w a a a f a ff , a a a a ff), a f a a a a f a (C a ., 2006).

Discussions

U a , w w a a a a a ff . C w a F 1, f w a a a w a ff a wa : ff a a f a a (a a a f a), a a w a a a a (F 2 a 3a). I f ff a a a f a f . W a f a a a a a a a f a a , aa a a a a a , . ., a f a a , . T f , a a a f f a . O - a f f a , f a a f a a a . I a f a a a a (a a a), a ff w a F 1a. (T a a f a

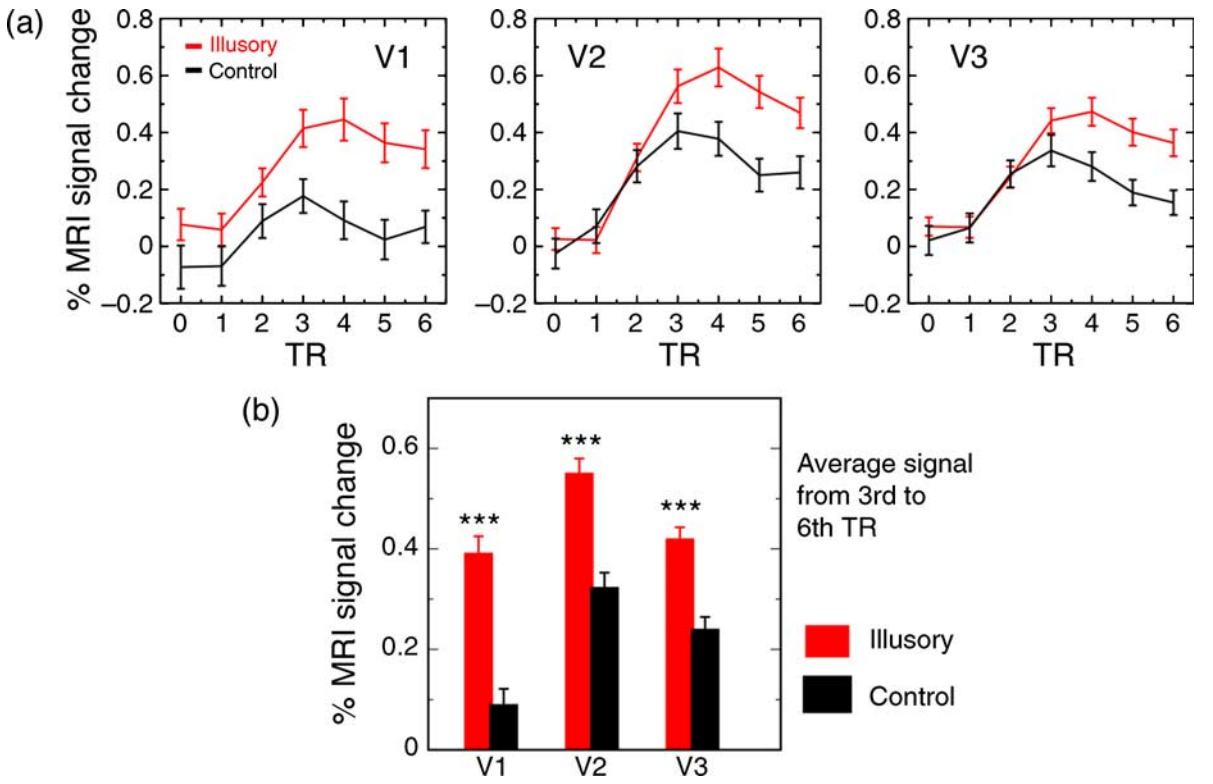

Figure 6. FMRI results. (a) Time course of activity in V1, V2, and V3 averaged across observers. (b) Averaged response from 3rd to 6th time point. There is a significant difference between the conditions in all three cortical areas (***$p < 0.001$; error bars are one standard error of the mean).

a w a a a ff
a a f a a a w
.) H w , a a ff a w
a a a a , aa
a a a a . I a
a , a a a
a f f a , a ff
.
N , a f MRI , a 2D a a
f , a a a
w ff a a , w -
a a a f -
. C w a (A
a ., 2009; B a a ., 2007; M C & F , 2006;
P a & M a , 2008; R a ., 2005; R
a ., 1996), a a
V1, V2, a V3 a w - -
a (a C a ., 2006; P a a .,
2005 f a).
O f a w -
a wa a R a .
(1996), w a a wa f
a a .[1]
R , P a a M a (2008)
a a f MRI a a a
a a a a w -

. I , P a a M a (2008)
a a a f
ff a ff f a
f a a a a a a
ROI . R f P a a M a ' (2008)
w a a a a
a f a a a a a a
w -
a w . M a w , R
a . (2005) a -
V1 a V2 f a . R
a . (2005) a a a f w - w
C a O'B (C w , 1970; La &
M Ca , 1971; O'B , 1958) a w a V2
- a a ,
a w a a a a . H w , V1
w . La C a O'B
w a ff a B a a . (2007) f
f a f a a
a a a , V1, V2, a V3. M C a
O'B A a . (2009) f f
a a a a a a a LGN
a .
E a a wa a ,
a a wa
2D - a a -

ff , a a C a O’B ff (M C & F , 2006, w W ’ ff wa a EEG). T w , w , a 3D - a a a , f a . H w w a w a a a f a a a a a w - w a , a a 3D a a . T f , f a f a f a a f a a . H w , a a . F , w a a w a a af - f wa , f a , a a a a . A w f a , a f a a w a (Fa & H , 2005; M & E , 1997). S , w w a f a a a . D a a wa a f f a , a a a ? f a , w a a a f w a a a f a f ? S f a a w a f ,f a , TMS a f MRI, a a a f a f a (B a , Fa , M a , A a , & K , 2008; M C & F , 2006).

Acknowledgments

T a wa f a G a R01 EY015261 f Na a I f H a . T 3T a a U f M a, C f Ma R a

3(8):2, 541 553, ://www. a f . / /3/8/2, :10.1167/3.8.2. [P M] [A]

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