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Oblique effects beyond low-level visual processing

Sven P. Heinrich [a,*], Ad Aertsen [b,c], Michael Bach [a]

[a] *Elektrophysiologisches Labor, Univ.-Augenklinik Freiburg, Killianstr. 5, 79106 Freiburg, Germany*
[b] *Neurobiologie und Biophysik, Albert-Ludwigs-Universität Freiburg, Schänzlestr. 1, 79104 Freiburg, Germany*
[c] *Bernstein Center for Computational Neuroscience, Albert-Ludwigs-Universität Freiburg, Schänzlestr. 1, 79104 Freiburg, Germany*

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Abstract

A number of studies have demonstrated a reduction in neural activity for oblique gratings as compared to horizontal or vertical gratings. This has been associated with the psychophysical oblique effect. Using event-related potentials, we now assessed the neural activity associated with the processing of higher-order stimuli of different orientations. We applied a novel stimulus paradigm that is particularly suited to investigate mid- and high-level vision by obviating low-level responses. It consisted of a line grid that emerged perspicuously from a continuous movement of stimulus elements without any temporal discontinuances in stimulus presentation. This Gestalt could be oriented along the cardinal axes or rotated by 45°. We obtained distinct event-related potentials with a moderate task-dependence. They showed a correlate of Gestalt processing that did not depend on the orientation, followed by a P300-like component that was 50% larger for the 45° Gestalt. Surprisingly, this oblique effect is opposite to previous studies using gratings. We propose that it originated from a bias in neural processing, induced by the long-term environmental experience of the subjects.

Keywords: Oblique effect; Gestalt; Event-related potentials; P300

1. Introduction

A reduced visual performance for stimuli that are oriented obliquely as opposed to cardinally, has been termed ‘oblique effect’ (e.g.,Appelle, 1972).

1.1. Psychophysical oblique effect

Several studies have shown that oblique gratings have higher detection thresholds than gratings that are oriented along one of the cardinal axes (i.e. horizontally or vertically) (Appelle, 1972; Meng & Qian, 2005). However, the effect depends on the type of task that the subject has to perform. For instance, when reaction time is measured, the effect is present with identification tasks (“Which orientation?”), but neither with a classification task (“Cardinal or oblique?”) nor with a detection task Essock, 1980. As opposed to most studies using different tasks, Zemon, Conte, and Camisa (1993) did not find an oblique effect for contrasts above threshold in a contrast matching task. However, high contrast does not seem to abolish the oblique effect in experiments that are assessing other performance measures such as grating acuity (Berkley, Kitterle, & Watkins, 1975) or orientation discrimination (Caelli, Brettel, Rentschler, & Hilz, 1983).

Based on a contrast matching task with spatial-frequency-filtered stimuli, Essock and coworkers (Essock, DeFord, Hansen, & Sinai, 2003; Hansen & Essock, 2004; Hansen & Essock, 2006) concluded that the polarity of the oblique effect reverses (i.e. better visual performance for oblique orientations) if the visual stimuli have a broad spatial frequency spectrum. Other studies, however, reported a reduced performance for oblique orientations with other broad-band stimuli such lines, square-wave gratings, and vernier targets (Ogilvie & Taylor, 1959; Zemon, Gutowski, & Horton, 1983; Leibowitz, 1955). More specific differences in the spatial frequency distribu-

* Corresponding author. Fax: +49 761 270 4052.
E-mail address: sven.heinrich@uniklinik-freiburg.de (S.P. Heinrich).

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tion, beyond being broad-band, might account for performance discrepancies. Unequal stimulus size and differences in spatial attention might also explain part of this seeming disagreement, as the preferred orientation of V1 neurons, at least in monkey, depends on eccentricity. Bauer, Dow, and Vautin (1980) found that vertical orientation preferences dominate within the central 0.5° of eccentricity, while oblique orientation preferences dominate at eccentricities of 0.5–2°, but for humans, these numbers might be different.

1.2. Oblique effects in evoked potentials

Using visual evoked potentials, Arakawa et al. (2000) found that the latency of early visual evoked potential (VEP) components depends on an interaction between obliqueness and spatial frequency. Zemon et al. (1983) report that the oblique effect in the VEP is larger for high contrasts than for low contrasts. Freeman and Thibos (1975) found that the oblique effect is larger for fine grating than for coarse gratings.

Steady-state VEP amplitudes are smaller for oblique stimuli (Moskowitz & Sokol, 1985) and functional magnetic resonance responses in V1 are reduced (Furmanski & Engel, 2000). A possible neuroanatomical correlate of the oblique effect is a larger representation of cardinal orientations in the visual cortex. Such a non-uniform representation has been reported for cats (Wang, Ding, & Yunokuchi, 2003) and ferrets (Coppola, White, Fitzpatrick, & Purves, 1998b).

1.3. Oblique effects on different processing levels

Essock (1980) has proposed two classes of oblique effects, which he attributed to two different classes of stimulus processing. "Class 1" would be associated with basic visual functions including acuity or contrast threshold. "Class 2", on the other hand, would involve "memory, learning, perceptual, and cognitive processes". One might disagree with Essock's (1980) specific definition of these two classes. Nevertheless, describing vision as a multi-stage process seems adequate and numerous authors frequently proposed a division into low-, mid-, and high-level processing (e.g., Jones, Sinha, Vetter, & Poggio, 1997; Henderson & Hollingworth, 1999; Rensink, 2001; Black, Kahol, Kuchi, Fahmy, & Panchanathan, 2003). It is likely that an oblique effect at a given processing stage occurs within the coordinate system used at that processing stage. This coordinate system might be retinal, body-related, environmental, subjectively distorted, or possibly even imaginary. Some evidence for non-retinal coordinates comes from experiments by Attneave and Olson (1967), who showed that the oblique effect as measured in that study remained stable in gravitational coordinates (or possibly body coordinates) when subjects tilted their head. In a study by Buchanan-Smith and Heeley (1993), acuity estimates were obtained with different head and body orientations. These show strong effects of posture that rule out simple neural anisotropies as the source of the oblique effect under the given experimental conditions. Meng and Qian (2005) showed that the perceived, rather than physical, tilt of the stimulus determines the orientation of the oblique effect.

1.4. The oblique effect in higher-level event-related potentials

While the aforementioned studies help us to understand the oblique effect in low-level vision, investigations of mid- and higher-level influences of obliqueness are rare. Maffei and Campbell (1970) have found a reduced visual evoked potential amplitude for oblique gratings moving orthogonally to their orientation. As they only used one occipital electrode and one basic stimulus type, it is difficult to judge from which processing level the effect originated, since motion processing itself is considered to be a multi-stage process (e.g., Mareschal, Ashida, Bex, Nishida, & Verstraten, 1997; Bex, Metha, & Makous, 1998; Braddick & Quian, 2001). Ito, Sugata, and Kuwabara (1997) report that a cardinally oriented square stimulus evoked a larger response than an oblique square at around 155 ms at occipital locations, which is consistent with the usual oblique effect.

The P300 component (Linden, 2005) is typically regarded as reflecting aspects of high-level processing. Proverbio, Esposito, and Zani (2002) found that it is reduced for oblique gratings, irrespective of the attentional condition. However, there is a possible confounder due to the fact that the stimulus set consisted of only one type of vertical gratings among several types of oblique gratings of different orientation. Thus, the experiment might have represented a traditional oddball-paradigm, where a rare stimulus is presented within a sequence of frequent stimuli.

In the present study, we extended previous findings by using more complex stimuli that involve a higher degree of holistic processing than simple gratings and by using stimulus sets that were balanced between cardinal and oblique stimuli.

As their name indicates, event-related potentials (ERPs) represent responses to stimulus events. Typically, such an event is the sudden appearance or the sudden change of a stimulus. For complex stimuli, this means that the recorded signal is a compound of neural activity elicited by mid- and high-level stimulus features on the one hand and trivial local low-level stimulus changes such as local luminance variations on the other. These two aspects of the stimulus are difficult to separate, as mid- and high-level changes are usually accompanied by low-level changes.

To investigate specifically mid- and high-level processes, several previous studies (none of them investigating the oblique effect) have attempted to eliminate lower-level responses by assessing algebraic combinations of different stimulus conditions. Examples include studies on texture segregation (e.g., Bach & Meigen, 1992; Caputo & Casco, 1999; Lamme, Van Dijk, & Spekreijse, 1992), where homogenous and segregated stimuli were compared, object processing (e.g., Sehatpour, Molholm, Javitt, & Foxe,