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Research Report

Spatiotemporal overlap between brain activation related to saccade preparation and attentional orienting

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ABSTRACT

Recent brain imaging studies provided evidence that the brain areas involved with attentional orienting and the preparation of saccades largely overlap, which may indicate that focusing attention at a specific location can be considered as an unexecuted saccade towards that location (i.e. the premotor theory of attention). Alternatively, it may be proposed that attentional orienting is simply relevant for preparing saccades, but the two processes may also be completely unrelated. In two experiments, we examined temporal activation of brain areas by measuring the electroencephalogram. Central cues indicated the likely side (left or right) at which a to-be-attended target would occur, or to which a saccade had to be prepared. Cue direction-related activity was determined, time-locked to cue onset. In addition, in our second experiment, delayed saccades had to be carried out, which allows to focus on processes strongly related to saccade execution. In nearly all tasks, an early directing attention negativity (EDAN), an anterior directing attention negativity (ADAN), and a late directing attention positivity (LDAP) were observed, time-locked to cue onset. Source analyses supported the view that this activity probably originates from areas within the ventral intraparietal sulcus (vIPS) and the frontal eye fields (FEF). The saccade-locked analysis also indicated that the FEF plays an important role in triggering saccades, but the role of vIPS appears to be minimal. The latter finding disfavors the premotor theory of attention, as it suggests that the relation between attention and action is less direct.

1. Introduction

Attentional orienting may be defined as the mental ability of selecting positions in space that are relevant for the control of our behavior, without necessarily shifting gaze, whereas saccade preparation may be characterized as the process that presets specific parameters relevant for the execution of saccades towards intended saccade goals. Regarding the functional relationship between these processes, three different viewpoints can be distinguished (for reviews, see Corbetta, 1998; Hoffman, 1998). First, Rizzolatti et al. (1987) proposed that attentional orienting might be identical to the planning of saccades: the premotor theory of attention. According to this view, attentional orienting activates the same brain areas as saccade preparation because attentional shifts are considered to be below-threshold activation of saccade motor programs. Secondly, attentional orienting and the planning of saccades may have functional overlap, for example, the locus of

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attention at a critical time point may provide crucial information for the accurate planning of saccades (Deubel and Schneider, 1996; Kowler et al., 1995). As a consequence, the brain areas activated while carrying out these functions may overlap, but additionally, task-specific activations are expected to be found. Finally, there need not be a functional relation at all; although attention is likely to be focused on the saccade goal, simply because this goal is interesting, it may fulfill no special role for the planning of a saccade (for suggestions in this direction, see Henderson et al., 1989). The latter view implies that different brain areas are expected to be activated while carrying out these functions, although some small overlap may be observed.

Results of PET (positron emission tomography) and fMRI (functional magnetic resonance imaging) studies point to large overlap in cortical brain areas between attentional orienting and the preparation and execution of saccades (Astafiev et al., 2003; Corbetta, 1998; Nobre et al., 2000a; Perry and Zeki, 2000). Considering these results together with several studies focusing on the areas involved with attentional orienting and spatial working memory (Corbetta et al., 2002), top–down attentional control (Hopfinger et al., 2000), and crossmodal spatial attention (Macaluso et al., 2003), it may be proposed that activity within two specific brain areas, the ventral intraparietal sulcus (vIPS) and the frontal eye fields (FEF), depends both on the direction at which attention is focused and the direction to which a saccade has to be prepared (e.g. see Astafiev et al., 2003; Corbetta and Shulman, 2002). This activation could reflect the coding of spatial locations in an effector-independent way, but, in line with the premotor theory of attention, it may also reflect activity arising from intended eye movements. Although both the vIPS and FEF have been shown to be involved during tasks requiring attentional shifts or the preparation of eye movements, their temporal interactions may differ between these tasks. Most of the aforementioned evidence with regard to the role of the vIPS and FEF has been derived from slow metabolic responses to neuronal activation, evolving over (tens of) seconds after neuronal activity (fMRI and PET). These techniques, although with rather precise localization accuracy, do not allow for the separation of events around attentional shifts and eye movements, which commonly occur in close succession (in the order of a few hundreds of milliseconds). Thus, the question may be raised whether the deployment of the vIPS and FEF over time is really comparable during attentional orienting and during saccade preparation. Using the EEG (electroencephalogram) enables a high temporal resolution and is therefore perfectly suited to give a more precise answer. Here, we focused on direction-related (or lateralized) EEG potentials in saccade preparation and covert orienting tasks as they provide specific information regarding spatial processing in these tasks and this method cancels out nonspecific differences in activation between tasks (e.g. due to differences in task difficulty).

Harter et al. (1989) examined the influence of attentional orienting on EEG by using arrow cues indicating the visual field in which stimuli to be detected appeared after a fixed interval. In this study and in modifications of this paradigm (Eimer, 1995; Hopf and Mangun, 2000; Nobre et al., 2000b; Van der Lubbe et al., 2005a; Yamaguchi et al., 1994, 1995), several direction-related ERP (event-related potential) components have been distinguished within this short interval. These components were determined after computing difference waves between ERPs evoked by left-pointing and by right-pointing arrows (e.g. Hopf and Mangun, 2000) or by computing contra-ipsilateral difference waves (in the current study), by extending the computation of the lateralized readiness potential (LRP) to all symmetrical electrode pairs with respect to arrow direction (e.g. Praamstra et al., 1996; Wascher and Wauschkuhn, 1996). The crucial aspect of the latter method is that activity unrelated to the relevant direction (e.g. general hemispherical differences) is additionally subtracted out (De Jong et al., 1988; Gratton et al., 1988), thereby providing a highly specific neuronal index. Three direction-related (or lateralized) ERP components have been distinguished. The earliest component, the early directing attention negativity (EDAN), is a negative (contralateral to arrow direction) deflection over occipital–parietal electrodes from 200–400 ms after cue onset. The EDAN has been replicated in several studies (e.g. Hopf and Mangun, 2000; Van der Lubbe et al., 2005a; Yamaguchi et al., 1994, 1995) and was mostly interpreted as reflecting voluntary arrow-induced shifts of visual attention towards the cued location. Recently, however, Van Velzen and Eimer (2003) found support for the view that the posterior EDAN at least partially reflects attentional selection of the side of the stimulus signaling the to-be-attended side (e.g. selection of the point of the arrow), rather than selection of the to-be-attended side. The second component, the anterior directing attention negativity (ADAN), an anterior negativity evoked at about 400 ms after cue onset (Eimer, 1995; Eimer et al., 2002; Nobre et al., 2000b; Yamaguchi et al., 1994, 1995) was hypothesized to reflect activity from premotor cortex. Finally, the third component, the late direction attention positivity (LDAP), a posterior positivity after about 500–700 ms, may reflect the influence of attention on processing along the ventral stream (Hopf and Mangun, 2000; but see Eimer et al., 2004; Näätänen, 1992).

Interestingly, quite similar components have been observed during both saccade preparation and the preparation of finger movements when the imperative stimuli cued by the arrows were presented foveally rather than peripherally (Jentzsch and Leuthold, 2002; Leuthold and Jentzsch, 2002; Van der Lubbe et al., 2000; Verleger et al., 2000; Wauschkuhn et al., 1997). For example, by employing a principal component analysis, Van der Lubbe et al. (2000) distinguished between several components in the direction-related ERPs while participants were preparing saccades and finger movements: one early negative parietal component, a later negative anterior component, and a third positive parietal component. Despite the methodological differences between both paradigms (e.g. regarding cue validity, the type of cues, the use of markers, etc.), the observed lateralized components in the aforementioned studies seem quite comparable to the earlier described EDAN, ADAN, and the LDAP. Thus, it may be hypothesized that saccade preparation and attentional orienting not only involve the same neural systems, but also show comparable activation patterns over time, which seems perfectly in line with the premotor theory of attention.