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Small saccades versus microsaccades: Experimental distinction and model-based unification

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ABSTRACT

Natural vision is characterized by alternating sequences of rapid gaze shifts (saccades) and fixations. During fixations, microsaccades and slower drift movements occur spontaneously, so that the eye is never motionless. Theoretical models of fixational eye movements predict that microsaccades are dynamically coupled to slower drift movements generated immediately before microsaccades, which might be used as a criterion to distinguish microsaccades from small voluntary saccades. Here we investigate a sequential scanning task, where participants generate goal-directed saccades and microsaccades with overlapping amplitude distributions. We show that properties of microsaccades are correlated with precursory drift motion, while amplitudes of goal-directed saccades do not dependent on previous drift epochs. We develop and test a mathematical model that integrates goal-directed and fixational eye movements, including microsaccades. Using model simulations, we reproduce the experimental finding of correlations within fixational eye movement components (i.e., between physiological drift and microsaccades) but not between goal-directed saccades and fixational drift motion. These results lend support to a functional difference between microsaccades and goal-directed saccades, while, at the same time, both types of behavior may be part of an oculomotor continuum that is quantitatively described by our mathematical model.

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1. Introduction

Our eyes move continuously to explore the world surrounding us, though we are mostly not aware of this fact. For inspection of stationary scenes, eye movements can be distinguished into saccades, ballistic eye movements that shift the gaze to a region of interest, and fixational periods, where almost all information processing on the fixated stimulus is achieved while the eye performs miniature or fixational movements (Haddad & Steinman, 1973; McCamy et al., 2014; Ratliff & Riggs, 1950; Steinman et al., 1973). Fixational eye movements are a superposition of three components (Ciuffreda & Tannen, 1995): (i) physiological drift, an erratic low-velocity motion, (ii) microsaccades, a ballistic high-velocity, small-amplitude movement, and (iii) tremor, a high-frequency oscillatory component (see Martinez-Conde, Macknik, & Hubel, 2004; Rolfs, 2009, for a review).

Microsaccades and saccades form an oculomotor continuum (Martinez-Conde, Otero-Millan, & Macknik, 2013; Otero-Millan et al., 2013; Zuber, Stark, & Cook, 1965). First, it is a

well-established observation that microsaccades and saccades share the same kinematic properties, although their amplitudes can differ by orders of magnitude: Both are binocular and conjugate behaviors (Ditchburn & Ginsborg, 1953) following the same linear relationship between amplitude and peak velocity (Cook, Stark, & Zuber, 1966; Zuber, Stark, & Cook, 1965). Second, neurophysiological work showed that neural activity in the superior colliculus, the top-level oculomotor structure of the midbrain (Sparks, 2002), is the key generation mechanism for saccades (Lee et al., 1988) and microsaccades (Hafed, 2011; Hafed, Goffart, & Krauzlis, 2009; Rolfs, Kliegl, & Engbert, 2008). Third, from a functional perspective, microsaccades contribute to precise relocation of gaze position in high-acuity visual tasks (Ko, Poletti, & Rucci, 2010) in a very similar way as saccades, even though microsaccadic gaze relocations are strongly limited in their spatial extents to less than a degree of visual angle.

Typically, the distinction between saccades and microsaccades is based on a more or less arbitrary amplitude threshold that varies considerably across studies (see, e.g., Martinez-Conde et al., 2009; Martinez-Conde, Otero-Millan, & Macknik, 2013, for a discussion). So far, however, no alternative criterion for the distinction between saccades and microsaccades has been proposed. Therefore, we set

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out to search for an alternative approach to the categorization of saccadic events. The rationale of our study is as follows. First, in a high-acuity observational task, we classify small saccades as goal-directed saccades or microsaccades. Second, we investigate statistical differences between both classes of events. Our definition of two separate saccade types would turn out to be arbitrary and useless, if statistical characteristics between both events types are indistinguishable, while reliable differences between event types would lend support to a new categorization of small saccades into subtypes.

While saccades are typically assumed to represent voluntary motor actions, microsaccades are considered as involuntary events (Yarbus, 1967). The strongest support for the involuntary nature of microsaccades comes from the statistical distribution of microsaccadic onset times, which follows an exponential distribution. The stochastic process that generates an exponential distribution is called a Poisson process which is characterized by constant probability over time for the observation of the next event (Cox & Miller, 1977). Since constant probability over time refers to complete temporal randomness, the exponential distribution of intersaccadic intervals for microsaccades supports the involuntary nature of this type of motor behavior. It is important to note, however, that the Poisson process might be modulated by additional processes for short inter-saccadic intervals and/or oscillatory components (Bosman, Womelsdorf, Desimone, & Fries, 2009; Engbert, 2006). In contrast to microsaccades, saccades do not produce an exponential distribution of inter-event times (Mergenthaler & Engbert, 2010). This can be taken as a statistical signature for stronger voluntary control of saccades compared to microsaccades. However, the labels *voluntary* and *involuntary* reflect interpretations rather than proven neurophysiological generating mechanisms. Therefore, we will introduce a task-dependent distinction between goal-directed saccades and microsaccades that is basically unrelated to the question of voluntary versus involuntary control.

How could both types of saccades statistically be differentiated? An elaborate theory on microsaccade generation needs to address potential interactions between drift (slow fixational movements) and microsaccades. Two peri-saccadic drift behavior have been reported. Post-saccadic drift is investigated well in larger saccades (Bahill, Hsu, & Stark, 1978; Collewijn, Erkelens, & Steinman, 1988; Weber & Daroff, 1972) and recently post-microsaccadic velocity of slow eye movements was reported to be increased compared to baseline velocity (Chen & Hafed, 2013).

Pre-microsaccadic effects were reported via five lines of evidence during sustained fixation. First, the inter-individual differences in microsaccade rates were correlated to the fractal dimension of precursory drift (Engbert & Mergenthaler, 2006). Second, retinal image slip was reduced immediately before microsaccades (Engbert & Mergenthaler, 2006), which was supported in videobased systems but not for coil systems (see discussion in Chen & Hafed, 2013). Third, amplitudes of microsaccades were modulated by precursory drifts (Mergenthaler & Engbert,

2010). For small saccades during prolonged fixation, Cherici et al. (2012) found that, fourth, faster drift generates more saccadic eye movements and, fifth, less self-compensatory drift motions are related to larger saccadic amplitudes. The first three pre-microsaccadic effects were not observed for larger saccades (Mergenthaler & Engbert, 2010) and the last two effects were not investigated for larger saccades so far. Therefore, a strong (functional) interpretation of the oculomotor continuum hypothesis (Otero-Millan et al., 2013) is currently not supported by experimental data, which indicates that there might be room for a possible refinement of the definition of microsaccades.

The motivation of the current work was to investigate relationships between drift and microsaccades in a laboratory task with overlapping amplitude distributions for microsaccades and small visually guided saccades. We suspected that a difference in statistical coupling of (micro) saccades and drift exists between small saccadic movements and microsaccades. In the experimental part of the current study, we developed a high-acuity task, where human participants were instructed to generate a series of saccades (Fig. 1, red color). These goal-directed (GS) saccades are aiming at a specific target stimulus, which is indicated by a participant via a color-dependent button-press. During intermediate fixations, however, spontaneous microsaccades (MS) are generated which lack an obvious movement target (Fig. 1, blue color). Due to overlapping amplitude distributions for GS and MS, our experimental paradigm permits a detailed comparison of movement statistics and, in particular, the statistical relationship between saccades and drift movements.

In general, we assumed to find stronger modulation of properties of GS (than of MS) by stimulus features (e.g., orientation of the stimulus, inter-stimulus distance). This hypothesis is based on the assumption that GS are driven by voluntarily invoked motor plans, while MS are a component of the fixational eye-movement system for controlling fixation. First, we expected longer saccade latencies for GS in the condition of short inter-stimulus distance compared to the long distance condition (Adams, Wood, & Carpenter, 2000; Kalesnykas & Hallett, 1994). Second, the direction of GS should be toward the next stimulus element. While recent results (Ko, Poletti, & Rucci, 2010) suggest that microsaccades might contribute to precise relocations of fixation position in high-acuity tasks, the distribution of microsaccadic orientations is expected to be broader than the corresponding distribution for GS. Finally, we hypothesize that GS are not statistically related to properties of slow drift movements (Mergenthaler & Engbert, 2010), while MS are expected to show such a coupling (Engbert & Mergenthaler, 2006).

Based on the experimental results, we will develop a mathematical model in the theoretical part of this study to test potential principles for the control of both saccade types observed in the experiment. Recently, we proposed an integrated computational model of fixational eye movements and microsaccades Engbert et al. (2011). In this model, drift is simulated by a self-avoiding
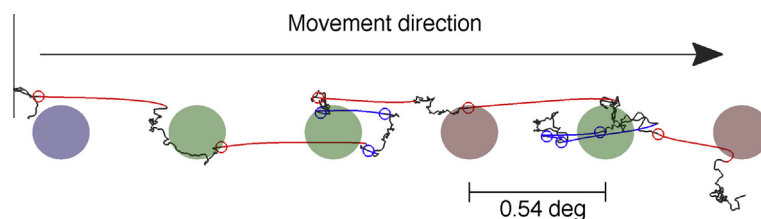

Fig. 1. Experiment on simultaneous observation of small saccades and microsaccades. (*Top*) Human participants are asked to produce a series of goal-directed saccades along a color-coded chain of fixation dots. (*Bottom*) A resulting eye trace consists of small goal-directed saccades (red) and microsaccades (blue) embedded in slower drift movements (gray). The circles indicate starting points for the saccadic movements. Participants had to signal the intended saccade target by pressing a computer key mapped to the color of the target stimulus.