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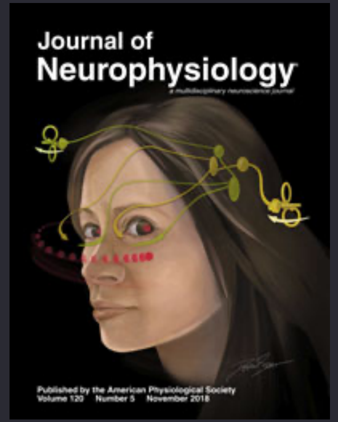

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ARTICLE

Faster processing of moving compared with flashed bars in awake macaque V1 provides a neural correlate of the flash lag illusion

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ical studies assume when interpreting the effect of speed in perceived spatial offset (Krekelberg and Lappe 1999; Murakami 2001; Nijhawan 1994; Whitney et al. 2000). Equivalent latency difference computed from the perceived spatial offsets from a recent psychophysical study (Wojtach et al. 2008), however, clearly decreases with speed (Fig. 15), similar to our findings. The discrepancy among the psychophysical studies can be reconciled by noting that Wojtach et al. (2008) used a wide range of speeds (up to 50°/s), whereas the previous studies used a narrow speed range (up to ~15°/s), which missed the full trend of the speed effect.

We found that the perceived spatial offset equivalent depended on speed and luminance (Fig. 7*D*, Fig. 9*C*, Figs. 12 and 13, *H*, and Fig. 14*G*), in line with psychophysical results (Fig. 7*E* and Fig. 9*E*). The magnitude of the perceived offset computed from the population decoding method appeared to be because our results build upon previously well-established psychophysical results on luminance manipulation (Lappe and Krekelberg 1998; Öğmen et al. 2004; Purushothaman et al. 1998) and are well in accordance with what would be predicted from them. Nevertheless, further experiments from naive subjects would be essential to confirm our human psychophysical results.

In our luminance manipulation experiment, we kept the background luminance near zero and changed only the bar luminance. This stimulus configuration, although suitable for mimicking flash lag psychophysical experiments, is not readily comparable to previous physiological studies in V1 that examined luminance or contrast effect on latency using different stimulus configurations (Carandini and Heeger 1994; Gawne et al. 1996; Maunsell and Gibson 1992; Oram 2010; Reich et al. 2001). Despite these stimulus differences, similar to the above

Fig. 14. Population multiunit activity decoding of flashes and moving bars and its relationship to flash lag psychophysics under luminance manipulation in *monkey L*. *A*: outlines of subset of receptive fields (red) of simultaneously recorded multiunits from a single representative session. Gray rectangles show the outlines of different flashes presented one at a time. *B*: flash decoding results; white box shown at *top* of each panel marks the horizontal position of flash in space and time. Luminance of the bars in each row is indicated on *left*. Colors of the plot indicate the average (across trials and sessions) probability [$p(S|\boldsymbol{R})$]of a horizontal bar position (*S*) given population activity at a given time (***R***). *C*: average probability of flash location, pooled across all flashes of a given luminance. *D*: average probability of moving bar position for different luminance values (columns) and directions (rows; L→R, motion from left to right; R→L, motion from right to left). White arrows indicate part of the motion trajectory (speed, 18°/s) that lies within the flashed region of space. White dots on the motion trajectory indicate moving bar centers. *E*: moving bar probability (rows in subpanels of *D*) aligned to the instantaneous horizontal position (white dots in *D*) of the moving bar center. For each speed and direction, the aligned probabilities were averaged across the instantaneous bar positions of the motion trajectory. *F*: latency of decoding flash and moving bar locations as a function of luminance. Flash latency (black trace) is the latency of peak of flash location probability in *C*. Moving bar latency (red trace) is the product of the spatial lag of the peaks of moving bar probabilities in *E* and the inverse of the speed. Error bars: 95% bootstrap percentile-based plug-in estimate of confidence intervals. *G*: luminance dependence of the latency difference (flash minus moving bar latency, *left* *y*-axis) and perceived spatial offset equivalent (*right* *y*-axis) obtained by the product of the latency difference and speed. Error bars as in *F*. *H* and *I*: latency difference and perceived spatial offset equivalent as a function of moving bar luminance (*H*) for a constant flash luminance (0.2 cd/m^2) or as a function of flash luminance (*I*) for a constant moving bar luminance (0.2 cd/m^2). Dashed line in *I* separates the luminance conditions that gave rise to perceived spatial offset equivalent corresponding to psychophysically measured flash lag (Lag) and flash lead (Lead) conditions. Error bars as in *F*. In *B* and *D*, for stimulus conditions under each luminance, color bounds were fixed at [0.1, 99.9] percentile. In *C* and *E*, traces of lighter shades with filled circles correspond to unsmoothed raw data. Median number of trials (sessions) = 132 (7), and median number of multiunits per session (total) = 39 (256).

studies, we also observed consistent increase in latency when the flash luminance was lowered. The latency for the moving bar also increased when the bar luminance was decreased. However, we unexpectedly found that luminance manipulation affected the latency of flash and moving bars differently. The latency profile of the moving bar response was not simply a downward-shifted version of the flash response latency profile. Instead, the increase in latency of the moving bar was much less pronounced compared with that of the flash when the luminance was low. With the caveat that we examined the luminance effect only in a single monkey, these results suggest that moving bars do not suffer as much processing delay as flashed objects under low-luminance conditions and likely invoke a different set of mechanisms in bringing out the observed latency effect.

Although several aspects of the flash lag illusion were

any relative position judgment nor trained in any other task like the present task; we still found a neural correlate of the illusion in V1. First, these results suggest that reporting relative position judgment is not necessary for observing a neural correlate of the flash lag illusion in visual area V1. Second, they argue against the current version of the motion-biasing model that involves only higher cognitive functions (Eagleman and Sejnowski 2007) and suggest that low-level mechanisms underlying the observed latency differences need to be taken into account.

While there is substantial evidence against the spatial extrapolation model at the psychophysical level (Baldo and Klein 1995; Brenner and Smeets 2000; Eagleman and Sejnowski 2000; Lappe and Krekelberg 1998; Purushothaman et al. 1998; Whitney and Murakami 1998), it is possible that spatial extrapolation could be happening at the level of V1. Given that