Recoding of sensory information across the retinothalamic synapse

SUPPLEMENTAL MATERIALS

Supplement A  Detection of spike trains from single retinal ganglion cells

In this study, we used either S-potential or whole-cell recordings from postsynaptic thalamic neurons to extract the pre- and postsynaptic spike trains (Wang et al., 2007). Even though the output of most thalamic relay cells is dominated by a single retinal input, relay cell may receive input from as many as six retinal afferents (Usrey et al., 1999). Since this paper focuses on information encoded by temporal correlations within spike trains of single RGCs, it was necessary to isolate the spike trains of the dominant RGC from each record. Otherwise, information that we attributed to temporal correlations might include the influence of convergent RGCs.

Thus, we took several measures to ensure that the retinal spike trains we used were from single RGCs. First, we only used data with S-potentials or postsynaptic events that formed a cluster distinct from noise (example in Figure 1B). Further, we generated histograms of inter-spike-intervals (ISIs) to confirm the presence of an absolute refractory period, as indicated by (nearly) empty bins below about 2 ms (population data in Figure S1E). In addition, we considered the possibility that the masking effect might create artifactual refractoriness (when two events occur very close to each other in time, their waveforms overlap and merge so that the sorting algorithm detects only one or even no events). We excluded this possibility by detecting spikes from two converging ganglion cells with displaced receptive fields (Figure S1A, C). The postsynaptic events from each cell formed distinct clusters (Figure S1B). Histograms of ISIs made from the events in each cluster revealed absolute refractoriness below 2 ms (Figure S1D, blue and green) whereas the plot made from the combined retinal spike trains did not (Figure S1D, gray). Rather, the masking effect created an empty bin at less than 0.5 ms, an interval far shorter than the biological refractory period.
Figure S1. *Identification of retinal spike trains from single ganglion cells.* (A) Whole-cell recording from a LGN relay neuron with two distinct retinal inputs. (B) Sorting of the two inputs and thalamic spikes. (C) Spatial receptive fields of the two retinal inputs and the thalamic output. (D) Inter-spike-interval distributions of the two retinal spike trains and the combined train. Red arrow marks the absolute refractory period (about 2 ms) and the black marks the time window (less than 0.5 ms) in which the overlap of the waveforms impairs the sorting of the two events. (E) Population data (n = 26) of the inter-spike-interval distributions of the detected retinal spike trains used in this study.
Supplement B  Sequential spike-triggered analysis of the retinal and thalamic spike train

In the main text of this paper, we have explained the idea of the joint relevant subspace as a framework to compare the pre- and postsynaptic encoding models with linear frontends. Here we describe how we identified the joint relevant subspace by means of sequential application of a system identification algorithm that maximizes mutual information. We used information-theoretic spike-triggered average and covariance (iSTAC) analysis (Pillow and Simoncelli, 2006) of responses to gaussian white noise. For an example joint relevant subspace, Figure 2A, we first identified features about which the retinal spikes were significantly informative (Figure S2B, solid blue). In this case, we identified only one significant retinal (presynaptic) feature. We then fixed this feature and identified an additional gained feature about which the thalamic spikes were significantly informative (Figure S2B, dashed red). The analysis identified no further features about which the retinal or thalamic spikes were informative. Therefore, the joint relevant subspace for this case is essentially two-dimensional. Likewise, we applied the space-time constrained iSTAC analysis (Pillow and Simoncelli, 2006) to the retinal and thalamic spike trains (Figure S2C). Consistent with our factorization analyses of the spatio-temporal structure of the joint relevant subspace (Figure 2), we found only one significant spatial filter but two significant temporal filters. Last, we performed conventional STA and STC analyses. The features identified using STA were almost identical to those identified using iSTAC. Hence, the simple spike-triggered average can be used to recover efficiently the two-dimensional joint relevant subspace for retinothalamic transmission.
Figure S2. **Sequential identification of the joint relevant subspace using the information-theoretic spike-triggered average and covariance (iSTAC) analysis.**  (A) The presynaptic and gained spatio-temporal features identified using the iSTAC analysis.  (B) Information content estimated during the two-step sequential application of iSTAC.  The first step (solid blue lines) identified a one-dimensional presynaptic subspace and the second step (dashed red lines) a one-dimensional gained subspace.  Light colored bars represent confidence intervals ($\alpha = 0.01$) obtained with bootstrap resampling.  (C) The spatial and temporal filters identified using a two-step space-time-constrained iSTAC analysis.
Supplement C  “Missing” retinal spikes – a control study

Pre- and postsynaptic events are combined in single channel when recorded using the S-potential or intracellular recording techniques. Thus, one faces the problem of sorting events from a mixed signal in which retinal inputs might be masked by postsynaptic spikes. Four examples of results obtained with our event sorting algorithm for one X cell pair are illustrated in Figure S3A. The first example shows an individual retinal event. The second and third cases depict instances in which the algorithm found retinal events that preceded thalamic spikes with varied but short (less than 1 ms) latencies. When, as for the fourth example, the algorithm failed to identify a retinal event at the foot a spike, it was possible that the retinal input was masked by a very rapidly evoked thalamic action potential. Consistent with this possibility, we found that typical synaptic latencies (as measured by cross-correlation analysis (Figure S3B) on the naively detected spike trains) are very short, less than 1 ms.

An earlier study in macaque provided a solution for this masking problem based on the assumptions that the spike waveforms can be replaced as a template and that the event waveforms sum linearly (Sincich et al., 2007). The conclusion of that analysis was that almost all thalamic spikes are preceded by a retinal action potential. Earlier work that we have done reached a similar conclusion, with the exception of spikes generated during thalamic bursts (Wang et al., 2007). Nevertheless, since bursts are rare, the assumption that each thalamic spike is causally related to a retinal action potential is reasonable in most cases.

Thus, it was necessary to determine if the masking effect introduced artifacts. Therefore, we generated retinal spike trains to which potentially missing retinal spikes were restored, as follows. We used two empirically identified constants (Figure S3B): the refractory period $t_{ref}$ and the masking latency $t_{lat}$. The former, 2 ms, was the biological absolute refractory period (Figure S3B, the dip before the correlation peak). The latter, 0.25 ms, was the synaptic latency below which the algorithm failed to detect retinal spikes. We restored the retinal spike train by replacing the missing retinal spikes per the following rule: a retinal event was added at $t_i - t_{lat}$ for each thalamic spike $t_i$ if there was no retinal event within the interval $(t_i - t_{ref}, t_i)$.

We used the restored retinal spike train to build a retinothalamic transmission model based on inter-spike-interval (ISI). The efficacy as a function of inter-spike-interval measured using the restored (Figure 6B) versus naive (Figure S3C) retinal spike trains were highly similar.

To test whether the restoration influenced our results, we substituted the restored for the naive retinal spike trains in all relevant analyses. All the effects we described in the main text held for analyses using the restored spike trains. (1) the joint relevant subspace is two-dimensional and the emergent thalamic selectivity to the gained feature is retained (Figure S3D); (2) single thalamic spikes are more informative than single retinal spikes, although the information about a specific feature might increase or decrease across the synapse (Figure S3E, F); (3) retinal spikes encode the joint relevant subspace with significant positive synergy at short inter-spike-times (Figure S3G-I).
Figure S3. “Missing” retinal spikes – a control study. (A) Four incidences of possible occurrence of retinal inputs during a “cell-attached” recording. The first case demonstrates a single retinal input and the second and third show retinal inputs detected right before thalamic spikes; in the last case the event sorting algorithm did not report a retinal input. (B) Conventional cross-correlation analysis of the retinal to the thalamic spike train. Vertical dashed lines mark two empirical time values used to place “missing” retinal inputs.
for the models in Figure 6, 7. (C) A Reconstruction of Figure 6B using the “naively” detected spike trains. (D-I) Reconstructions of Figure 1F, Figure 3C, Figure 4A, Figure 5B, Figure 5A, top and Figure 5C using the modified retinal spike trains in which the “missing” spikes were recovered.
Supplement D  Pair-wise synergy in the joint retinothalamic feature space

We have shown that, information about the *gained* feature is implicitly encoded by retinal spike correlations and is then recoded, by means of temporal summation, into an explicit single spike code. It might seem that all information is recoded into single spikes in the LGN, leaving no room for thalamic spike pairs to serve as potential coding elements (*Figure 4D*). However, this is not the case, as we explain with the following argument. Even though a retinal spike is less informative than a thalamic spike about the whole feature space, it can be more informative about certain specific features (*Figure 3C*). Likewise, the synergy might not be zero for certain features even though it is zero about the whole relevant subspace. *Figure S4* shows the pre- and postsynaptic synergy of the example X cell pair in *Figure 4A*. It is readily apparent that thalamic spike pairs with various inter-spike-times can encode additional information about certain features. In particular, the selectivity to the *lost* feature can be recovered if thalamic spike pairs are regarded as elements of coding. Therefore, if downstream (cortical) neurons also shift selectivity in the feature space, thalamic pair-wise correlations might indeed be exploited despite a zero synergy.

For the reason stated above, the overall mutual information and synergy of a spike train might not help understand recoding across a synapse. This is because the change of information and the synergy about certain feature subspace can greatly vary if there is a shift of the relevant feature space across the synapse.
Figure S4. **Pair-wise synergy in the joint retinothalamic feature space.** (A, B) Retinal and thalamic pair-wise synergy within the joint feature space. Information and synergy conveyed by single and pair of spikes are visualized as polar plots on the two-dimensional joint feature space. Data were analyzed for the same RGC-LGN cell pair illustrated in the main figures. Left column: twice the amount of single-spike information in gray and the amount of spike-pair information as colored curves; right column: positive synergy lobes in bright color and negative in dark. Vertical position represents inter-spike-time.
Supplement E  Estimates of the upper and lower bound of single-spike information

Mutual information between the stimulus \( s \) and the response (spike, in our case) can be estimated in two alternative ways, either expressed in terms of stimulus or of response distributions:

\[
I[\text{spike}; s] = E_{p[\text{spike}, s]} \log_2 \frac{p[s|\text{spike}]}{p[s]} = E_{p[\text{spike}, s]} \log_2 \frac{p[\text{spike}|s]}{p[\text{spike}]}
\]

The equality of these two expressions derives from Bayes’ Theorem; the operator \( E \) here denotes expectation.

**Lower bound**

In the *Results*, we used the estimate based on stimulus distributions (see *Materials and Methods*:)

\[
I[\text{spike}; s] = E_{p[\text{spike}, s]} \log_2 \frac{p[s|\text{spike}]}{p[s]} = \left( \frac{p[s|\text{spike}]}{p[s]} \log_2 \frac{p[s|\text{spike}]}{p[s]} \right)_s
\]

It is rarely possible to make a direct estimate because the high dimensionality of the stimulus calls for more experimental data than are usually available; hence, reasonable approximations must be made. Thus, we identified a low-dimensional feature space (represented by a basis, or bases, \( B \)) of the high-dimensional stimulus \( s \), and estimated a lower bound of \( I[\text{spike}; s] \):

\[
I_B[\text{spike}; s] = \left( \frac{p[x|\text{spike}]}{p[x]} \log_2 \frac{p[x|\text{spike}]}{p[x]} \right)_x \leq I[\text{spike}; s]
\]

Here \( x = s \cdot B \) is a low dimensional projection of the stimulus.

The information theoretic characterization of a feature space with reduced dimensionality is, essentially, a search for \( B \) such that \( I_B[\text{spike}; s] \) best approaches \( I[\text{spike}; s] \) (Sharpee et al., 2004; Pillow and Simoncelli, 2006). For our analyses, we used both information theoretic (Pillow and Simoncelli, 2006) and the spike-triggered (Schwartz et al., 2006) analyses to identify feature spaces \( B \).

Further, we used a less data-demanding, but also less tight, estimate of the lower bound \( \hat{I}_B[\text{spike}; s] \leq I_B[\text{spike}; s] \) (see *Materials and Methods*), based on the assumption that \( p[x|\text{spike}] \) and \( p[x] \) are gaussian distributed.

**Upper bound**

The second estimate of \( I[\text{spike}; s] \) does not rely on a stimulus subspace and can thus be estimated directly from the spiking response (Brenner et al., 2000); however, multiple trials are often needed in order to estimate the firing rate:

\[
I[\text{spike}; s] = E_{p[\text{spike}, s]} \log_2 \frac{p[\text{spike}|s]}{p[\text{spike}]} = \left( \frac{p[\text{spike}|s]}{p[\text{spike}]} \log_2 \frac{p[\text{spike}|s]}{p[\text{spike}]} \right)_s
\]

\[
= \left( \frac{r(t)}{\bar{r}} \log_2 \frac{r(t)}{\bar{r}} \right)_s
\]

\[
= \frac{1}{T} \int_0^T \frac{r(t)}{\bar{r}} \log_2 \frac{r(t)}{\bar{r}} dt
\]
Here  \( r(t) \) is the instantaneous firing rate and \( \bar{r} \) the mean firing rate; \( T \) is the duration of the trial. The last equality replaces integration over stimulus by integration over time under the assumption of ergodicity. This is a true estimate of \( I[\text{spike}; \mathbf{s}] \) and serves as an upper bound for the information content that can be decoded from single spikes.

**Comparing the lower against the upper bound**

To evaluate the quality of our estimate of the lower bound for the information encoded by single spikes, we compared it with estimates of the upper bound. We had sufficient data to estimate the upper bound for 7 RGC-LGN cell pairs (4 X-type and 3 Y-type), as illustrated for an example cell pair, **Figure S5A-C** (note that our figures are similar to **Figure 2A-C** in (Brenner et al., 2000)). Note that we previously tested the validity of this procedure for linear extrapolation (adopted from (Brenner et al., 2000)), by performing empirical tests that used surrogate data modeled from spike trains recorded in LGN (Koepsell and Sommer, 2008).

We then compared estimates of the lower and upper bounds for the same 7 cells, **Figure S5D** (for RGC) and **Figure S5E** (for LGN). For all 7 cell pairs analyzed, the lower bound was, on average, at 69% of the upper bound for RGC and 73% for LGN. Next, we plotted the single-spike information for the LGN against that for the RGC (**Figure S5F**), c.f. **Figure 3A**. Here, each cell pair is represented by a rectangular “box”; the left and right edges mark the lower and upper bounds of RGC information whereas the bottom and top edges mark the lower and upper bounds for LGN. In all cases, the “boxes” lie entirely above the diagonal, suggesting that even the lower bound of LGN information is higher than the upper bound of RGC information. Therefore, the lower bound estimate we used in our study (see **Results**) was sufficiently tight.
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Figure S5. **Estimates of the upper and lower bounds of single-spike information.** (A) Estimate of the upper bound of single-spike information for an RGC-LGN cell pair as a function of the size of the time bin; circles and crosses represent estimates obtained with 60 and 30 trials, respectively. Light colored lines are linear extrapolations of information content for time bin approaching zero. (B) Information estimation in A as a function of number of trials; lines extrapolate to an infinite number of trials. (C) Estimates of variance of information in B, using shorter segments of the whole stimulus sequence. Deviations of information estimation as a function of stimulus length follows the inverse square-root law (light colored lines). A, B and C are directly analogous to Figure 2 of (Brenner et al., 2000). (D, E) Comparison of upper versus lower information bound for 7 RGC-LGN pairs (4 X type and 3 Y type) where multiple trial data were available; the upper bound is plotted against the lower bound (as shown in Figure 3A) for RGC spikes (D) and LGN spikes (E). (F) Estimated ranges of single-spike information for the 7 cell pairs. Each box represents a cell pair; the left and right edges mark the lower and upper bound estimated for RGC spikes whereas the bottom and top edges mark the lower and upper bound for LGN spikes.
Supplement F  Single-spike information rate across the retinothalamic synapse

We found that single spikes in the LGN are more informative than those in the retina, consistent with an earlier study (Sincich et al., 2009). We also observed a substantial (about three-fold) reduction in the number of spikes across the retinothalamic synapse. Thus, it seems that the retina emits more numerous but less informative spikes than the LGN. But how do RGCs compare to relay cells in terms of the amount of information conveyed per unit time (i.e. information rate)? This question has been addressed by estimating information rates for single spikes. However, these estimates might not provide a clear answer, as we now explain.

We illustrate information rates for single retinal and thalamic spikes in Figure S6A (same population as in Figure 3A; note that retinal rates were adjusted to correct for events potentially obscured by thalamic spikes (see Supplement C) and might be overestimated). In addition, we plotted rates of information about features within the joint feature space. We illustrate the results for 3 example cell pairs (Figure S6B-D) that correspond to the points circled in Figure S6A. The changes in information rates across the synapse were diverse, ranging from significant reduction (Figure S6B), to approximate conservation (Figure S6C), to significant increase (Figure S6D). (Sincich et al., 2009) reported the results of a similar analysis (see Figure 2D in (Sincich et al., 2009)); in their case no points lay significantly above the diagonal, a distribution they thought reflected the theoretical limit imposed by the “Data Processing Inequality” (DPI) (Cover and Thomas, 1991). Even though most of our results are similar to theirs (most of the data points in our sample fell just below the diagonal) two points fell significantly above that line, Figure S6A. In the following we explain why these points need not violate the DPI.

First, the rate of single-spike information (or more generally, of single-symbol information) does not reflect the actual rate of information that a spike train conveys. That is, even if the stimulus-RGC-LGN cascade were Markovian, single-spike information could appear to violate the DPI when it actually does not. We illustrate this with a binary process that is transformed by two consecutive temporal filters and estimate information rate analytically or by using simple simulations.

Consider a cascade of three point processes: \( \mathbf{X} = \{X_t\} \), \( \mathbf{Y} = \{Y_t\} \) and \( \mathbf{Z} = \{Z_t\} \) that strictly obey Markovity:
\[
\mathbf{X} \rightarrow \mathbf{Y} \rightarrow \mathbf{Z}
\]
Let \( \{X_t\} \) be independent and identically distributed (i.i.d.) binary variables obeying a Bernoulli (binary) distribution of \( p = \frac{1}{2} \) \( (P[X_t = 0] = P[X_t = 1] = \frac{1}{2}). \) Further, define the statistical dependencies from \( \mathbf{X} \) to \( \mathbf{Y} \) and from \( \mathbf{Y} \) to \( \mathbf{Z} \) as the following deterministic temporal filtering:
\[
Y_t = X_{t-1} \lor X_t \\
Z_t = Y_{t-1} \land Y_t
\]
where \( \lor \) and \( \land \) denote logical “or” and “and” operations, respectively. The information rates conveyed by single symbols (defined below) seemingly violate the DPI (\( I'[\mathbf{X}; \mathbf{Y}] \geq I'[\mathbf{X}; \mathbf{Z}] \)):
\[
I_{ss}'[\mathbf{X}; \mathbf{Y}] = I[\ldots, X_{t-1}, X_t; Y_t] = 0.8113 \text{ bit/time step} \\
I_{ss}'[\mathbf{X}; \mathbf{Z}] = I[\ldots, X_{t-1}, X_t; Z_t] = 0.9544 \text{ bit/time step}
\]
Note that the processes are stationary so the estimates are independent of \( t \).
The true information rates should be defined as either of the following, similar to the entropy rates (Cover and Thomas, 1991):

\[
I'[X; Y] = \lim_{t \to \infty} \frac{1}{t} I[X_1, X_2, \ldots, X_t; Y_1, Y_2, \ldots, Y_t] \\
= \lim_{t \to \infty}\{I[X_1, X_2, \ldots, X_t; Y_1, Y_2, \ldots, Y_t] - I[X_1, X_2, \ldots, X_{t-1}; Y_1, Y_2, \ldots, Y_{t-1}]\}
\]

For stationary processes, the two limits stated above exist and are equal. For our specific example, we estimated:

\[
I'[X; Y] = I'[X; Z] = 0.6992 \text{ bit/time step}
\]

Therefore, the DPI is not violated.

There is a reason why the estimates for single-symbol information rate \(I_{ss}'\) might appear to violate the DPI. When temporal filtering introduces synergy or redundancy in the code, information for single symbols deviates from the true rate.

Second, the stimulus-RGC-LGN cascade is not Markovian. Each thalamic relay cell is not only influenced by its dominant retinal afferent, but other convergent input such as strong inhibition (Wang et al., 2007). Such additional input might contribute to the total amount of information that a relay cell transmits.
Figure S6. Single-spike information rate (information content per unit time) across the retinothalamic synapse. (A) Information about the joint feature space encoded by single spikes per unit time. Data are from the population illustrated in Figure 3A. Potentially missing RGC spikes were added back to the retinal spike trains (see Supplement C and Figure S3) before analysis. The three red circles mark the three example cells illustrated in B-D. (B-D) Information rates conveyed by RGC and LGN spikes about specific features within the joint feature space are illustrated for three example RGC-LGN cell pairs: the X cell pair in Figure 3C (B) and two other examples (C and D), conventions same as in Figure 3C. LGN spike trains can be either more or less informative than RGC spike trains about either the entire feature space or specific features within it.
Supplement G  Dimensionality of LGN feature space

The dimensionality of the feature space that a neuron detects indicates the complexity of the neural code. Our study identified only one significant dimension for the presynaptic feature space (the presynaptic feature, or filter). The postsynaptic feature space was also one-dimensional, even though we used two filters, the presynaptic and gained, to describe the responses in the LGN. We explain this apparent conflict below.

To define the joint relevant subspace (see Materials and Methods), we first identified the one-dimensional feature space for the RGC (the presynaptic feature), and then added a second feature (the gained feature) to account for responses in the LGN. This process yielded a two-dimensional joint feature space that subsumed the features encoded by the RGC and the LGN. A plot of the thalamic information accounted for by the two-dimensional joint feature space versus the one dimensional feature space (Figure S7A, B) shows a significant gain (average 46%) from the presynaptic to the joint feature space (Figure S7A). Note that there was no gain of information from the one-dimensional postsynaptic feature to the joint feature space (Figure S7B), indicating that the dimensionality of the thalamic features was no higher than for the retinal ones. We illustrate this finding with polar plots (e.g. Figure S7C) in which one-dimensional information (two-lobed curve, gray crosses) overlays the two-dimensional information (light colored circle, black crosses). The one-dimensional information about the presynaptic feature (blue arrow) is significantly less than the two-dimensional amount; however, both quantities are similar for the postsynaptic feature (red arrow). Thus, the dimensionality of features in the LGN remains one.

An earlier study of retinothalamic transmission in the primate (Sincich et al., 2009) identified two filters (temporal features) for each retinal and thalamic neuron. By contrast, we identified only one significant filter for both types of cells in the cat. Could we have missed additional (less informative) features, perhaps because of an insufficient amount of data on our part? Establishing the significance of features about which only a small amount of information is conveyed requires more data than for highly informative ones. However, the amount of data we acquired was comparable, if not greater than, that which (Sincich et al., 2009) recorded.

All told, it seems likely that disparities between our work and that of (Sincich et al., 2009) reflect species differences. For example, the difference in the retinal and thalamic temporal features we identified in cats was much larger than those in primate (Sincich et al., 2009). Additional discrepancies between the two studies might have resulted from the stimuli used; ours were uncorrelated (white noise) and theirs were correlated (naturalistic sequences).
Figure S7. *Thalamic single-spike information about joint (two-dimensional) versus single (one-dimensional) features.* (A) Information conveyed by single LGN spikes about the two-dimensional joint feature space plotted against that about the presynaptic feature. (B) Information conveyed by single LGN spikes about the two-dimensional joint feature space plotted against that about the postsynaptic feature. (C) *Figure 3C* (main text) modified to show the LGN single-spike information within the joint feature space; gray and black crosses mark the information about single (pre- or postsynaptic) versus the joint features.
Supplement H  Temporal features encoded by retinothalamic spikes probed by different stimuli

Do the temporal features we identified depend on the structure of the stimulus displayed? To address this question, we compared results obtained with two patterns of gaussian white noise, a 2D checkerboard and a 1D target pattern (Figure 2A) updated at two rates, 72 Hz or 48 Hz. In all 6 pairs we tested (Figure S8A-F), the temporal features probed by 2D and 1D patterns were similar. Further, the similarity was maintained across frame rates (compare Figure S8A-D with Figure S8E, F) and is even preserved across different update rates (Figure S8F).

In sum, the temporal features we identified with white noise stimuli were similar. However, we do not expect that temporal features recovered from responses to white noise versus stimuli with correlated statistics would be the same since the early visual system adapts to stimuli with different statistics (Lesica et al., 2007).
Figure S8. Temporal features estimated by using gaussian white noise stimuli with different spatial organizations and frame rates. (A-F) For 6 example cell pairs, temporal features (presynaptic and gained shown) extracted by using stimuli with 2D checkerboard (dark thin lines) versus 1D target pattern (light thick lines) spatial organizations. Stimuli used in A, B, C and D were updated at 72 Hz; stimuli in E were updated at 48 Hz; the 1D stimulus in F was updated at 72 Hz and the 2D stimulus was updated at 48 Hz. Conventions are the same as in Figure 2B and Figure 3E.
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REFERENCES


