different response harmonics: $A_{m1}$ and $A_{m2}$ are the amplitudes of the harmonic responses associated with the motion feature in surfaces 1 and 2, respectively; $A_{c1}$ and $A_{c2}$ are the amplitudes of the harmonic responses associated with the color feature in surfaces 1 and 2, respectively; $M1$ and $M2$ refer to conditions in which subjects tracked the motion of surfaces 1 and 2, respectively; and $C1$ and $C2$ refer to conditions in which subjects tracked the color of surfaces 1 and 2, respectively.

To demonstrate the analysis and the competing feature- vs. object-based predictions, we simulated the response of 200 voxels with random motion and color biases (Fig. 2). To do so, we modeled each voxel as comprising 16 feature-selective channels: 8 for motion and 8 for color. Each channel was assigned a random weight so that the population response exhibited randomness for both direction of motion (Fig. 2A) and color (Fig. 2B). We simulated each voxel’s response by the sum of the responses of the underlying channels plus noise (Fig. 2C). Averaging the amplitude spectrum across all 200 simulated voxels reveals the harmonic response to each stimulus component (Fig. 2D). The amplitudes labeled $A_{m1}$ and $A_{m2}$, at 22 and 25 cycles/scan, refer to the motion harmonics to surfaces 1 and 2, respectively, and $A_{c1}$ and $A_{c2}$, at 28 and 19 cycles/scan, refer to the corresponding color harmonics. The feature-based hypothesis predicts that attention will modulate the response to the cued feature. The object-based hypothesis predicts that attention will modulate the response to the cued feature and to the other feature of the same surface. We modeled these two alternatives by appropriate gain changes in the response of the underlying channels (see Methods, Simulation). Figure 2, E and F, shows the time course of the response and the corresponding amplitude spectrum when feature-based attention was directed to the motion of surface 1 (M1). As expected, feature-based attention enhances the amplitude of the motion harmonic in surface 1 ($A_{m1}|M1$) relative to the other stimulus components. Figure 2G shows the time course associated with the effect of object-based attention. In this case, amplitudes associated with both the motion and color of surface 1 ($A_{m1}|M1$ and $A_{c1}|M1$) are enhanced.

We used a similar methodology to analyze the data collected from the scanning sessions. We collapsed the responses across all voxels within each visual area and then averaged across subjects to make an overall qualitative assessment of the effects of attention on harmonic responses (Figs. 3–7). The between-subjects averaged amplitude spectrum for V1 is shown in Fig. 3 for each attention condition. Figure 3A shows the amplitude spectrum when the motion of surface 1 was tracked (M1). In this condition, $A_{m1}|M1$ was weakly enhanced relative to the neighboring noise response, suggesting that attention to M1 could enhance the response to the corresponding feature. This qualitative enhancement was not present for the motion in surface 2 ($A_{m2}|M1$), suggesting that our observation is not due to spatial attention or nonspecific enhancement of direction-selective mechanisms in V1. When subjects tracked the motion of surface 2 (M2), $A_{m2}|M2$ appears to have been enhanced, rising above the surrounding noise relative to $A_{m1}|M1$, and $A_{m1}|M2$ appears to have been reduced in amplitude compared with $A_{m1}|M1$ (Fig. 3B). These results indicate that, in V1, the effect of feature-based attention to the direction of motion is surface specific.

When subjects attended the color of either surface, the color harmonics in V1 ($A_{c1}|C1$ and $A_{c2}|C2$) do not appear to have risen above the surrounding noise (Fig. 3, C and D). Surprisingly, however, attention to color of a given surface seems to have enhanced the responses associated with the motion of that surface: in the C1 and C2 conditions, respectively, $A_{m1}|C1$ (Fig. 3C) and $A_{m1}|C2$ (Fig. 3D) appears to be greater than the noise harmonics. In fact, the overall pattern of amplitude responses across the four stimulus frequencies looks similar regardless of whether the subjects track the motion or color of a surface (Fig. 3, A vs. C, and B vs. D). These results suggest that the observed modulations in V1 BOLD responses are associated with surface-specific attentional selection for the direction of motion.

Fig. 3. Average amplitude spectrum of V1 hemodynamic responses under each attention condition. Each panel shows the amplitude spectrum of the hemodynamic responses averaged across the 6 subjects. Error bars show SE of the mean across the 6 subjects. A: amplitude spectrum when subjects were cued to track the motion of surface 1 (M1). The amplitude of the harmonic response associated with the motion of surface 1 shown in black ($A_{m1}|M1$ at 22 cycles/scan) was higher than the harmonic response associated with the motion of surface 2 ($A_{m2}|M1$ at 25 cycles/scan). In this condition, the harmonic responses to the color, shown in dark gray ($A_{c1}|M1$ at 19 cycles/scan for surface 1 and $A_{m2}|M1$ at 19 cycles/scan for surface 2), are comparable to the response amplitude at nonstimulus harmonics (gray). B: same as A for the condition in which subjects were cued to track the motion of surface 2 (M2). C and D show similar measurements for when subjects tracked the color of surfaces 1 (C1) and 2 (C2), respectively.