

## “Extinction” of the McCollough effect does not transfer interocularly

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A McCollough effect was induced in subjects by having them view typical adapting stimuli binocularly for 5 min. In the control condition, the strength of the McCollough effect was measured 20 min after the end of the adaptation. The strength was measured during monocular and binocular viewing of a test pattern via a color cancellation technique. Monocular strengths for the two eyes of a given subject were equal to each other and slightly weaker than the binocular strength. In the test condition, 15 min of the 20 min between adaptation and testing were spent monocularly viewing black and white gratings of the same orientation and spatial frequency as the adapting gratings. The strength of the effect as measured ipsilaterally was markedly decreased from that in the control condition. The strength of the effect as measured with the contralateral eye showed only a small decrease from that of the control condition. This finding is relevant to various models of the McCollough effect and related color aftereffects, especially those that posit a “learning” type of mechanism between achromatic spatial channels (which exhibit clear interocular transfer of various achromatic effects) and monocular color channels.

When McCollough (1965) first reported the orientation-contingent color aftereffect that bears her name, she noted that the effect was monocular, in the sense that viewing the adapting pattern with only one eye results in a strong effect in the adapted eye but no effect in the other eye. It is even possible to generate oppositely colored effects in corresponding parts of the visual fields of the two eyes in a given subject. These findings about the monocular-ity of the McCollough effect have been replicated many times (e.g., Murch, 1972; White, Petry, Riggs, & Miller, 1978).

In contrast, various achromatic phenomena related to spatial frequency channels do transfer interocularly. Successive spatial frequency contrast (Blakemore & Sutton, 1969; Meyer, 1974), successive orientation contrast (also called the tilt aftereffect; Movshon, Chambers, & Blake-more, 1972), and change in contrast sensitivity following adaptation (Bjorklund & Magnussen, 1981; Blake & Cormack, 1979; Blakemore & Campbell, 1969; Selby & Woodhouse, 1981) all show considerable interocular transfer. When measured quantitatively, the interocular effects are typically 70% of the ipsilateral monocular effect.

Achromatic gratings have been related to the McCollough effect in both experimental and theoretical contexts. Experimentally, they have been shown to cause a decrease in the strength of an existing effect. That is, after building up a McCollough effect, subsequent viewing of achromatic gratings of the same frequency and orientations

speeds up the decay of the effect (Skowbo, Gentry, Timney, & Morant, 1974). In fact, the work of Holding and Jones (1976) and Jones and Holding (1975) suggests that the viewing of achromatic gratings is essential for the decay process.

Theoretically, it has been suggested that the McCollough effect itself is a manifestation of some sort of contiguity learning between an achromatic spatial system (e.g., spatial frequency channels) and a color system. This idea has been presented in various forms over the years. Murch (1976) examined the possibility that the McCollough effect was a form of classical conditioning. McCarter and Silver (1977) argued against such a view because of clear differences between the McCollough effect and traditional examples of classical conditioning. Murch (1977) recognized these differences, but argued that the similarities were more important. More recently, Skowbo and Forster (1983) and Skowbo and White (1983) presented further arguments against a classical conditioning model of the McCollough effect. Skowbo (1984) presents a complete review of the question and takes the position that there are sufficiently many differences between the McCollough effect and traditional examples of classical conditioning to justify a conclusion that they not be considered the same. On the other hand, Skowbo explicitly mentions the possibility that the McCollough effect might be due to some more primitive kind of associative learning than classical conditioning.

In an independent review (Savoy, 1984), I reached the same conclusion about classical conditioning, but I also argued for the usefulness of some kind of contiguity learning model in conceptualizing the McCollough effect. The discussion below is taken largely from that review paper. The representation chosen to present the ideas is sugges-

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tive of many neuronally based learning theories (especially Grossberg, 1982), but this connection is not critical in the present context. See Savoy (1984) for other representations and more motivation for choosing the present one.

Figure 1 is a schematic representation for a contiguity learning model of the McCollough effect. The achromatic spatial system is activated whenever a luminance grating of the appropriate orientation and spatial frequency is presented. The precolor system is activated by the presentation of color. (The name "precolor" is chosen because it is clear from other considerations that the site of the McCollough effect is peripheral to the ultimate sensation of color.) Whenever the spatial system is active, it sends (weak) inhibitory signals to all the precolor systems. Finally, there is a process that controls the strength of the inhibitory connections. On a short time scale, the strength of the inhibitory signal depends on the strength of the signal from the achromatic spatial system and the strength of the connection. Note that the strength of a *signal* is different from the strength of a *connection*. The strength of the signal from the achromatic channel is controlled by the achromatic contrast of the stimulus. This signal is multiplicatively gated by some process presumed to correspond to the strength of the connection. The product of signal strength and connection strength forms the net inhibitory signal that reaches the precolor system. The precolor system also receives (much stronger) direct ex-

citatory input from peripheral, wavelength-selective channels.

The strength of the (inhibitory) connection from a given achromatic spatial unit to a given precolor unit is represented schematically by the size of the semicircle. Figure 1a represents the situation before McCollough effect adaptation; Figure 1b, the situation after adaptation. Three things control the strength of the connection. First, concurrent (or nearly concurrent) activity in the achromatic spatial system and a precolor system will cause the strength of the connection in the semicircle between them to grow. This is analogous to contiguity learning: the strength grows in response to the contiguous activity of two nearby systems. Second, the strength will spontaneously decay to some baseline level, but this occurs at a very slow (possibly zero) rate. This is analogous to spontaneous decay of learning. Third, the strength will decay fairly rapidly when there are signals from the spatial system in the absence of strong, concurrent activity in the nearby precolor system. This is analogous to extinction in classical conditioning. While this decay rate is more rapid than spontaneous decay, it is not as rapid as the rate at which effects can be built up during adaptation to colored gratings.

The details of this kind of model can be specified more quantitatively, but such detail is irrelevant in the present context. The model is simply serving as a convenient way to represent certain ideas. The only features that are critical are: (1) the existence of independent achromatic spatial and precolor systems; (2) some kind of contiguity learning between these systems, such that a color signal from some sort can be generated by activating the achromatic spatial system alone; and (3) a decay process analogous to extinction in the sense that activity of the achromatic spatial system alone increases the decay rate.

Now I will connect the above model with the experimental observations made at the beginning of this introduction. The McCollough effect is monocular. How, in the context of a "learning"-type model, is this monocularity going to be represented? One possibility is that there are simply two copies of each type of system, one for each eye, as shown in Figure 2. While this has the desired properties with respect to the McCollough effect as discussed so far, it requires that the achromatic spatial systems involved must be different from those involved in various experiments concerning achromatic gratings, because two independent copies do not provide a mechanism for interocular transfer. On grounds of parsimony, it would be nice if the achromatic spatial systems involved were the same; only one achromatic spatial system would then be needed instead of two. Furthermore, there is circumstantial evidence in that direction. The orientation bandwidth and spatial frequency bandwidths of the McCollough effect and the various achromatic spatial frequency effects are roughly equal (the evidence for this being summarized in Skowbo, Timney, Gentry, & Morant, 1975). The model shown in Figure 3

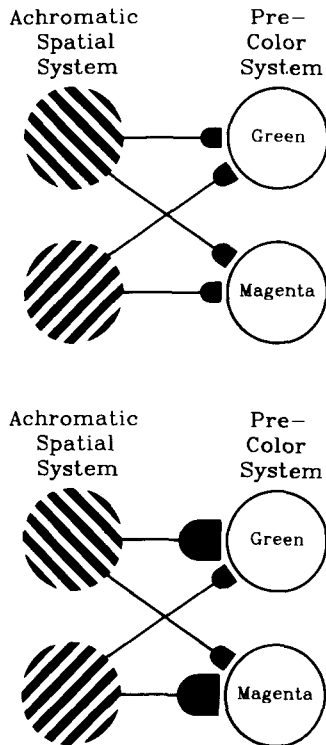


Figure 1. A schematic representation for a contiguity learning model of the McCollough effect (a) before adaptation and (b) after adaptation. See text for details.

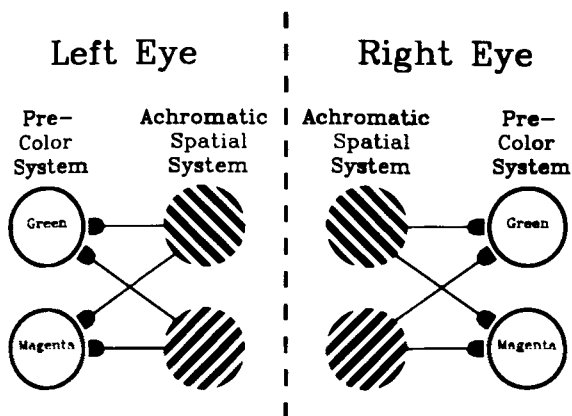


Figure 2. An extension of Figure 1 that represents the fact that the McCollough effect does not transfer interocularly.

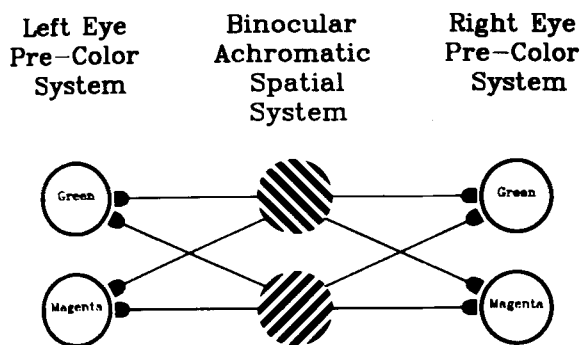


Figure 3. An alternative extension of Figure 1 that represents both the fact that the McCollough effect does not transfer interocularly and the fact that many achromatic spatial frequency effects do transfer interocularly.

is an attempt to get the best of both worlds. The achromatic spatial systems are binocular, and can thus exhibit interocular transfer, whereas the precolor systems are monocular, and thus provide for independent monocular McCollough effects.

The key point about Figure 3 is that it immediately suggests the present experiment. Although the McCollough effect continues to be monocular, the model predicts that extinction of the McCollough effect should show interocular transfer. That is, assuming a purely binocular achromatic spatial system (i.e., one that would show 100% interocular transfer) and assuming the existence of a mechanism analogous to extinction, monocular viewing of achromatic gratings should speed up the decay in both eyes for a binocularly induced McCollough effect.

**METHODS**

The four subjects (including the author) had normal color vision and very good color discrimination, as tested on the Farnsworth-Munsell 100-Hue Test. Two subjects were aware of the purpose of the experiments and two were not.

The subject, seated in a chair, viewed the test and adapting stimuli in a dark room. He/she was positioned behind a set of mirrors and black velour baffles so that each eye saw only half of the stimulus display. This allowed for control of which halves of the stimulus display contained the test or adapting patterns. Each eye could thus be tested or adapted separately as well as simultaneously, and it was not necessary to close or occlude an eye during monocular presentations. Neither artificial pupils nor bite bars were used.

Adapting and test patterns were displayed on a Mitsubishi RGB color television monitor driven by a 512 x 512 pixel resolution frame buffer (International Imaging Systems Model 70F). Luminance of the test pattern was 65 cd/m<sup>2</sup>. Luminance of the adapting patterns was as great as the equipment allowed: 65 cd/m<sup>2</sup> for magenta, 130 cd/m<sup>2</sup> for green, and 185 cd/m<sup>2</sup> for white. The adapting pattern subtended 8° of visual angle from the viewing distance of 68 cm. Each adapting pattern was a circularly masked, green-and-black or magenta-and-black square-wave grating of 2 cpd.

The color cancellation task was performed as follows. The subjects moved a trackball horizontally to change the color of the test pattern (shown in Figure 4). Trackball motion caused green light to be added to one orientation of line and an equal amount to be subtracted from the other orientation. The amount of red and blue light was simultaneously adjusted for each orientation so that the calculated CIE luminance of both test areas remained constant (and equal to that of the fixed achromatic annulus). Thus, the subject changed saturation along one hue dimension (magenta/green), but could not change the luminance of either test area. The subject was instructed to make the color of the two orientations as close to equal as possible. This was reported to be an easy task. In most cases, the resulting test pattern stripes were not only equal to each other, but also neutral, that is, the same achromatic percept as for the fixed annular surround. On a few occasions, when a particularly strong aftereffect was generated, the resulting stripes in the test pattern were slightly colored relative to the surrounding annulus. Even in these cases, however, the criterion of minimizing the color difference between orientations was reported as very easy. The magnitude of the color effect was calculated in terms of the difference in color between the two orientations (+45° and -45° gratings), using the CIE L,u\*,v\* system (Wyszecki & Stiles, 1982).

Each experimental session consisted of four parts. First, the subject repeatedly adjusted a test pattern to look neutral. This test pattern was presented binocularly, monocularly to the left eye, and

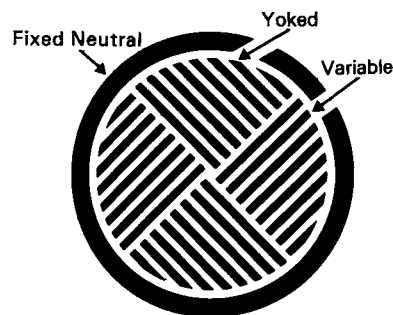


Figure 4. The test pattern that was used to measure the strength of the McCollough effect. Subjects moved a trackball that controlled the intensity of the green television phosphor in the "variable" grating. Any addition of green light there was accompanied by subtraction of the same amount of green light from the "yoked" grating. Simultaneously, the amount of red and blue light was automatically adjusted so that the calculated CIE luminance of both test areas remained constant (and equal to that of the "fixed," achromatic annulus). Thus, subjects changed saturation along one hue dimension (magenta/green), but could not change the luminance of either test area. Subjects were instructed to make the color of the two orientations as close to equal as possible.

monocularly to the right eye, four times each. Each test pattern was presented with a small, random amount of magenta or green light added to the orientations, so the subjects could not assume that the pattern was neutral before they started making their adjustments. Second, the subject viewed, binocularly, 5 min of typical McCollough-effect-inducing patterns: 5-sec presentation of green and black bars, oriented at  $+45^\circ$ , alternated with 5 sec of magenta and black bars oriented at  $-45^\circ$ . Third, the subject spent 15 min in one of two viewing conditions. In the control condition, the subjects viewed nothing; they just sat in the dark room. In the test condition, they viewed square-wave gratings of the same frequency and alternating orientation as the adapting patterns, but black and white instead of black and magenta or black and green and presented to one eye only, not binocularly. The subject then viewed nothing for several minutes. Finally, 20 min after the end of the color adaptation, there was another sequence of adjusting test patterns to look neutral.

Four subjects were run through this sequence four times each. Each subject viewed the black and white stimuli in the left eye for two sessions and the right eye for two sessions. The pairing of color and orientation during adaptation was alternated from session to session (e.g., green,  $+45^\circ$  gratings would be used in one session, while green,  $-45^\circ$  gratings would be used in the next). Thus, oppositely colored effects were generated from session to session.

At least 48 h elapsed between sessions for individual subjects. In most cases, this was sufficient to eliminate any residual effect from the previous adaptation. In any case, any remaining effect was measured by the preadaptation settings. These preadaptation settings were used as the baseline neutral for measuring the strength of the next settings after adaptation.

Two additional experiments were run in which, during the 15 min that one eye viewed black and white diagonal gratings, the contralateral eye viewed (instead of a dark field) either a uniform disk of the same luminance as the diagonal bars or horizontal and vertical bars of the same luminance and spatial frequency as the diagonal bars.

It should be noted that, although the averages and standard deviations to be described below reflect the major portion of the data, there were occasional sessions in which very little effect was found. That is, in a few experimental sessions, the measured results in the ipsilateral and contralateral eyes were roughly equal, and both showed less decrease from the control condition than the ipsilateral eye normally showed. The net effect of including these sessions in the averages is to make the difference between ipsilateral and contralateral eyes smaller. The difference is still great enough, even with these trials, to justify the conclusions drawn.

## RESULTS

Figure 5 shows the data for the control condition of darkness only between adaptation and test. The binocular effect has been normalized to 100%. The monocular effects are roughly 70% as strong. For the test condition (of monocularly presented black and white gratings between adaptation and test patterns), it will make sense to compare monocularly and binocularly measured effects with themselves, rather than with the binocular effect only. Figure 6 shows the results for the test condition. The ipsilateral eye shows only 25% of the strength that it would have shown if darkness had intervened, instead of the black and white gratings. The contralateral eye shows 80% of its original strength. Thus, there has been little interocular transfer. More specifically, there has been little transfer relative to the amount shown in other, achromatic experiments, and there has been little transfer rela-

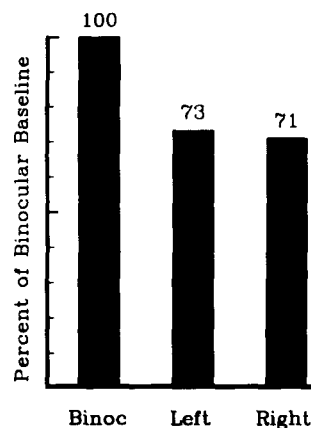


Figure 5. Data for the control condition of darkness only between adaptation and test. The values shown are the magnitude of the color difference between the two orientations in the test pattern, relative to some standard. The standard chosen is the strength of the binocular effect, which has therefore been normalized to 100%. The monocular effects are roughly 70% as strong. In absolute terms, the binocular effect has a value of 16.1 plus or minus a standard deviation of 3.9 in  $L, u^*, v^*$  units. This is the difference between the preadaptation color difference settings ( $-1.35 \pm 2.1$ ) and the postadaptation color difference settings ( $15.2 \pm 3.8$ ). These averages are over two trials each for four subjects. Intersubject variability is greater than intrasubject variability.

tive to the amount predicted by the model shown in Figure 3.

The data in Figure 6 are the average over four trials for each of four subjects. The mean  $\pm$  one standard deviation of the effects are as follows: for the ipsilateral eye,  $25 \pm 14$ ; for the contralateral eye,  $80 \pm 17$ . Note that

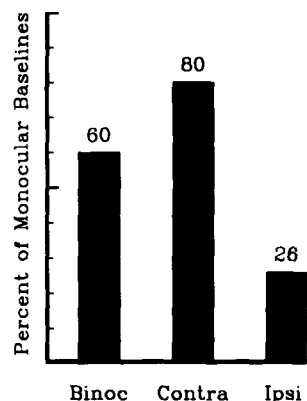


Figure 6. Results for the basic experiment. The values shown are the ratios (expressed as a percentage) of the color difference in the test condition compared with that for the corresponding control condition of Figure 5, averaged over four trials for each of the four subjects. The ipsilateral eye shows only 25% of the strength that it would have shown if darkness had intervened, instead of the black and white gratings. The contralateral eye shows 80% of its original strength. Thus, there has been little interocular transfer. More specifically, there has been little transfer relative to the amount shown in other, achromatic experiments; and there has been little transfer relative to the amount predicted by the model shown in Figure 3.

all these numbers are percentages of the effect in the control condition.

One question that might be raised concerning this experiment is whether the use of darkness on the contralateral eye during monocular exposure to the black and white gratings might result in a spurious lack of interocular transfer. The argument (presented in general terms by Lehmkuhle & Fox, 1976, for example) is that monocular exposure might actively shut down (perhaps via some kind of binocular-rivalry-induced suppression) any system that would otherwise show interocular transfer. Thus, even though binocular systems capable of showing interocular transfer might exist in the context of the present experiment, their activity might be suppressed because of the drastic asymmetry of stimulation to the two eyes during monocular exposure to the critical black and white adapting gratings.

To address the preceding issue, two additional control experiments were run with two of the subjects. These experiments were identical to the test condition above, except that something other than darkness was presented to the contralateral eye during the 15 min of monocular exposure to the black and white gratings. In one case, the contralateral eye saw a uniform luminance disk that subtended the same visual angle as the outline of the black and white gratings. In the other case, the contralateral eye saw square-wave gratings of the same spatial frequency, but of 0° and 90° orientation. In both cases, the basic result was the same: there was a substantial decrease in the color aftereffect in the ipsilateral eye and much less change in the contralateral eye.

## DISCUSSION

The data are clear. Whatever is being done to the McCollough effect during monocular viewing of achromatic gratings, it shows little or no interocular transfer. What does this imply for modeling?

There were two fundamental assumptions in generating the prediction that motivated the present experiment. The first was that achromatic spatial systems are exclusively binocular. The second was that something analogous to "extinction" of learning is triggered by the viewing of achromatic gratings. Together, these assumptions imply interocular transfer of extinction. Since extinction does not transfer, one or both of these assumptions must be incorrect.

There is evidence from other experiments to suggest that the "exclusively binocular" assumption for the achromatic spatial system is untenable. For example, Vidyasagar (1976) has been able to generate conflicting monocular and purely binocular McCollough effects at the same time. I have replicated that finding, although the effects were very weak relative to the usual McCollough effect strength. Nonetheless, the existence of any such effects requires, in the context of the present class of models, the existence of both binocular and monocular achromatic spatial channels. Indeed, Vidyasagar's work implies the

existence of *preferentially monocular* spatial systems. Related work of Wolfe and Held (1981, 1982) on the tilt aftereffect (successive orientation contrast) requires the existence of *preferentially binocular* spatial systems.

The status of "something analogous to 'extinction'" is less clear. Is it "extinction" or competition between competing, differently colored McCollough effects that accounts for the influence of achromatic adapting patterns? The extinction idea has been presented in the introduction. The competition idea is that adaptation to achromatic gratings builds up McCollough effects for *all* colors, thus diluting the previously established effects. The question of which kind of idea makes more sense for the McCollough effect remains unresolved. (Skowbo & Clynes, 1977, also mention the possibility of an "achromatic" McCollough effect in a similar context.) I discuss these issues in some detail in the review paper mentioned previously (Savoy, 1984), but the conclusion is unchanged—whatever the process involved, it is not identical to extinction as defined by classical conditioning, but there is insufficient evidence to choose between a competition model and an extinction type of model.

In any case, the present experiment rules out the model shown in Figure 3. The fact of substantial interocular transfer of achromatic spatial effects rules out the model in Figure 2, at least if the achromatic spatial system is taken to be the same one that exhibits 70% interocular transfer in other contexts. If, as I argue elsewhere (Savoy, 1984), the ME is to be understood as a consequence of *changes in the strength of interaction* between two relatively independent systems—one concerned with achromatic, oriented, spatial-frequency-specific form and the other with color—then any model that attempts to represent our current knowledge must include a detailed analysis of the various binocular, monocular, interocular, and dichoptic phenomena associated with the ME (of which the present experiment is but one example). Such a model will undoubtedly require a collection of spatial systems with various degrees of monocular and binocular specificity. This will come as no shock to neurophysiologists (e.g., Hubel & Wiesel, 1962, 1968; Schiller, Finlay, & Volman, 1976), but I emphasize that the arguments and data that led to this position in the present setting are exclusively psychophysical.

In pursuing more complete models, we must consider both qualitative and quantitative issues. Qualitative issues include the fact that there is no representation (in Figure 2 or Figure 3) of the various spatial contrast effects (such as simultaneous and/or successive spatial frequency contrast and simultaneous and/or successive orientation contrast). There is also no way to account for binocular rivalry in either spatial or color systems. It is likely that many of these effects would result from the judicious addition of simple inhibitory connections between various of the spatial systems. Some of these connections might have other implications, such as might be relevant to another major issue that is beyond the scope of the present class of models—stereopsis.

Quantitative issues are obvious. How can we get estimates of the strengths of the various systems, especially the spatial systems? Wade and Wenderoth (1978) examined models and data arising from other people's studies of the tilt aftereffect, but showed that the relative, quantitative predictions they could extract from the models were not consistent with their own data. This modeling was, as recognized by all those involved, based on very simplified models. In particular, there was no representation of preferentially monocular or binocular systems. The McCollough effect has both unique promise and unique problems for the study of quantitative effects. On the positive side, the effect is stronger and much longer lasting than most aftereffects. This alone is sufficient to make it an attractive candidate for quantitative work. Furthermore, its simultaneous connection with form and color, and with monocular and binocular issues, such as evidenced by the present work, adds to its interest. But there are considerable difficulties—although these, too, are not without promise of their own. Numerous studies (e.g., Amure, 1978; Lund & MacKay, 1983; MacKay & MacKay, 1975, 1977; Shute, 1979) have demonstrated that general metabolic activity, as influenced by such drugs as caffeine, alcohol, and nicotine, and as influenced by such things as sleep and sleep deprivation, have a definite impact on the magnitude and decay rate of the McCollough effect. Some of these factors may account for the occasionally large day-to-day variability of the McCollough effect strength for a given subject (although variability between subjects is even greater). In order to use the McCollough effect to obtain meaningful quantitative estimates of the relative strengths of the various spatial systems, it will be essential to have a better understanding of the influences, metabolic and otherwise, that control this variability.

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