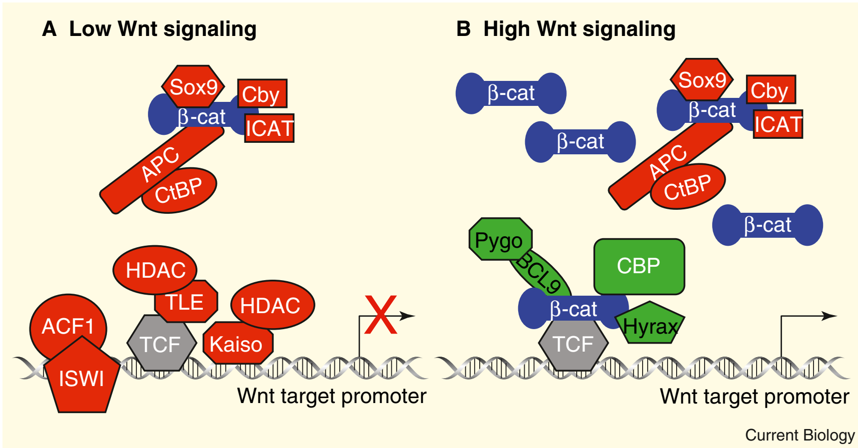

Figure 3. The TCF transcriptional switch mediating activation of Wnt targets.

In the absence of signaling (A), TCF represses Wnt targets by recruiting co-repressors such as TLE/Gro. Other repressive complexes also contribute to this silencing. In addition, there are several factors that act as 'nuclear β-catenin buffers' which prevent β-catenin–TCF interaction when β-catenin is present at low concentrations. On Wnt signaling (B), the high level of nuclear β-catenin overcomes these buffers, and β-catenin displaces the repressors from the target gene chromatin. β-catenin dependent recruitment of a variety of co-activators allows transcription to proceed.

Indeed, while *pygo* is essential for Wnt regulation of targets in flies, mice lacking both *pygo* genes have a much more modest reduction in Wnt target gene expression. At the general level, however, the idea that β-catenin switches a TCF from a transcriptional repressor to an activator is a useful way to think of Wnt-mediated regulation of many target genes. While invertebrate TCFs clearly contain both the repressive and activating activities — essential in flies and worms which only have one TCF each — it appears that some vertebrate TCFs have become more specialized, with TCF3 possessing mainly silencing activity and LEF1 functioning in the activation portion of the transcriptional switch.

It should be noted that there are many genes that are downregulated in response to Wnt signaling, and in some cases it has been confirmed that a TCF–β-catenin complex directly mediates this repression. How many of the genes downregulated by Wnt–β-catenin signaling are directly repressed remains an important unanswered question. The mechanism of TCF–β-catenin repression has not been worked out in detail, and it appears to be different among the few genes studied in detail. The diversity of mechanisms by which β-catenin can regulate gene expression likely explains how this pathway can perform so many essential functions throughout the animal kingdom.

Further reading

Cadigan, K.M., and Liu, Y.I. (2006). Wnt signaling: complexity at the surface. J. Cell Sci. *119*, 395–402.

Eaton, S. (2008). Retromer retrieves wntless. Dev. Cell *14*, 4–6.

Guder, C., Philipp, I., Lengfeld, T., Watanabe, H., Hobmayer, B., and Holstein, T.W. (2006). The Wnt code: cnidarians signal the way. Oncogene *25*, 7450–7460.

Kikuchi, A., Kishida, S., and Yamamoto, H. (2006) Regulation of Wnt signaling by protein-protein interaction and post-translational modifications. Exp. Mol. Med. *38*, 1–10.

Logan, C.Y., and Nusse, R. (2004). The Wnt signaling pathway in development and disease. Annu. Rev. Cell Dev. Biol. *20*, 781–810.

Mikels, A.J. and Nusse, R. (2006). Wnts as ligands: processing, secretion and reception. Oncogene. *25*, 7461–7468.

Parker, D.S., Blauwkamp, T., and Cadigan, K.M. (2007). Wnt/β-catenin-mediated transcriptional regulation. In Wnt Signaling in Embryonic Development, Vol. 17, Sokol, S., (ed), Advances in Developmental Biology, Wassarman, P.M. (ed). (San Diego: Elsevier), pp. 1–61.

Polakis, P. (2007) The many ways of Wnt in cancer. Curr. Opin. Genet. Dev. *17*, 45–51.

Städeli, R., Hoffmans, R., and Basler, K. (2006). Transcription under the control of nuclear Arm/beta-catenin. Curr. Biol. *16*, R378–R385.

Zeng, X., Huang, H., Tamai, K., Zhang, X., Harada, Y., Yokata, Y., Almeida, K., Wang, J., *et al.* (2008). Initiation of Wnt signaling: control of Wnt coreceptor Lrp6 phosphorylation/activated via frizzled, disheveled and axin functions. Development 135, 367–375.

Department of Molecular, Cellular and Developmental Biology, University of Michigan, Ann Arbor, Michigan 48109-1048, USA.
E-mail: cadigan@umich.edu

Correspondences

Perceptual mislocalization of bouncing balls by professional tennis referees

David Whitney, Nicole Wurnitsch, Byron Hontiveros and Elizabeth Louie

The perceived position of a moving object depends on the object's motion and the motion of other objects in the scene [1]. Here, we report a real-world example of how this causes a perceptual error for professional tennis referees, which players could exploit to their advantage.

A relatively new rule in professional tennis allows players to challenge referee calls. As long as the player continues to challenge incorrect referee calls, the player is allowed to continue making challenges. In the 2007 Wimbledon championship, there were over 140 player challenges, and more than 25% of these resulted in overturned calls. Clearly, challenges make a difference in the outcome of tennis matches. Successfully challenging calls allows players to continue making challenges, and it therefore behooves players to challenge only those calls that they believe are clearly in error.

Although it is well known that moving objects are misperceived as being shifted in the direction of their motion ([2,3]; see also Supplemental References in the Supplemental Data available online with this issue), these kinds of perceptual errors have rarely been documented in sports [4–6]. To measure whether referees accurately perceive the position at which a tennis ball bounces, we reviewed randomly selected Wimbledon tennis matches (4,457 total points) and recorded each case in which a tennis ball landed close to or on a line (Figure 1; see also the Supplemental Experimental Procedures). On each recorded trial (point), three trained observers independently rated whether the ball landed on or off the

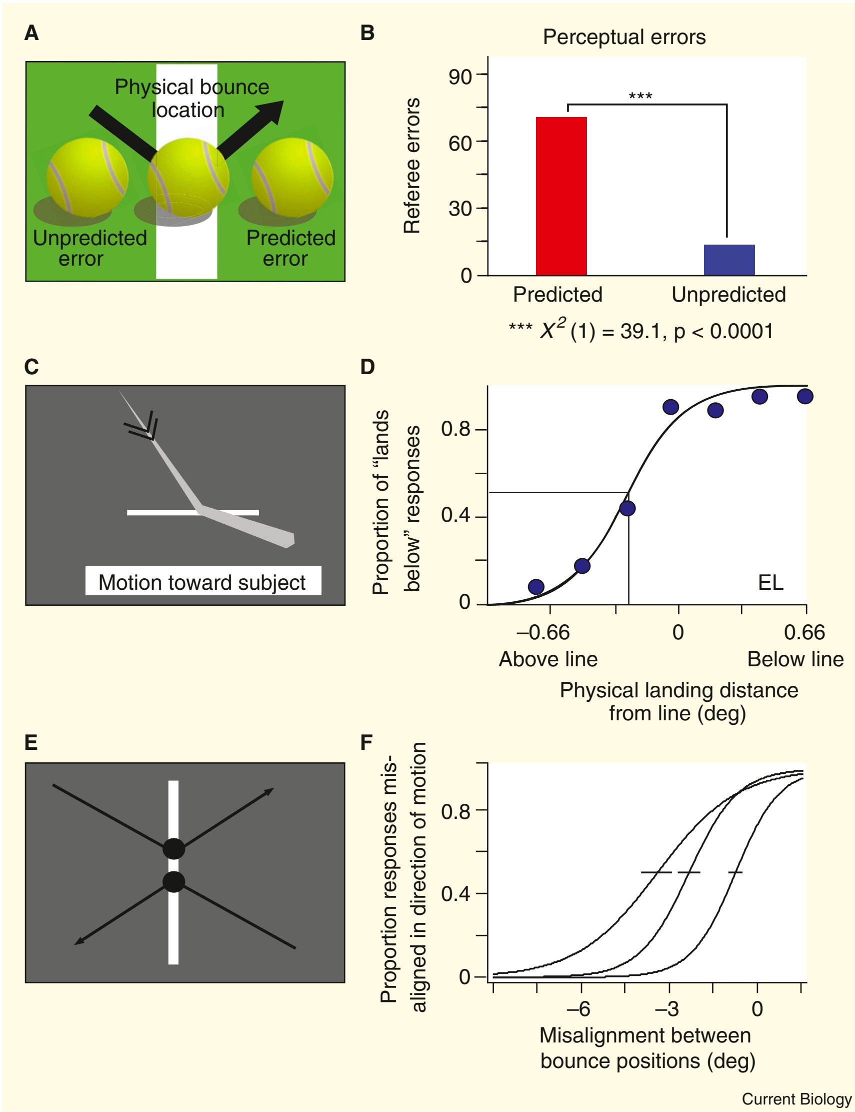

Figure 1. Perceptual mislocalization of bouncing tennis balls by line judges.

Tennis balls that physically bounce on a line (A) are not always judged accurately; some balls are erroneously reported as being shifted in the direction of the ball's motion ('predicted error') or opposite the direction of the ball's motion ('unpredicted error'). If unbiased, misjudgments of both types should be equally likely. Of a random set of 4,457 points drawn from the 2007 Wimbledon championship, referees made 83 erroneous judgments. Of these, the majority (84%) were errors in which the ball was reported as being shifted *in* the direction of the ball's motion ('predicted errors'). (B) This perceptual bias is significant ($X^2(1) = 39.1$, $p < 0.001$). The bias was also present for those points that were challenged by players and arbitrated by instant-replay (Figure S1). (C) Stimuli for one condition of a psychophysical experiment that measured the perceptual localization of bouncing objects. A translating and expanding dot simulated motion toward the observer. (The grey trace highlights one possible trajectory but was not visible in the experiment.) A representative psychometric function (D) for one subject shows that an object simulating motion toward the observer had to bounce physically above the horizontal line to appear as if it bounced on the line. The perceived shift in the bounce position of moving objects was significant across subjects ($p < 0.01$). A second psychophysical experiment (E) revealed that two objects traveling toward each other and bouncing in physical alignment appear misaligned, each appearing shifted in the direction of motion by a significant degree ($p < 0.01$) (F). Also see Supplemental Figures S2 and S3.

line — in or out of play; a ball that lands on a line, even a tiny fraction of the line, is still considered in play. We also analyzed all available instant-replay videos (for example, those recorded by the 'Hawk-Eye' system used during the matches to arbitrate challenged calls).

Because of the nature of the tennis court, there are two kinds of errors that are primarily made when a ball is called in or out of play: a ball could physically bounce in the court but be called out, or a ball could physically bounce out of the court but be called in. If tennis referees were bias-free, they would be equally likely to make each of these two kinds of errors. But if referees have the same perceptual bias found in psychophysical experiments [1], we would expect that they will judge more tennis balls as being out (when actually in, a 'predicted' error) than in (when actually out, an 'unpredicted' error). That is, if there is a perceptual mislocalization of the bouncing tennis ball, there should be significantly more 'predicted' errors than 'unpredicted' errors (Figure 1A). We found that this prediction was true: referees called many more balls out that were actually in play than vice versa (Figure 1B).

Most points ended without a tennis ball bouncing near a line, so the perceptual judgments required by referees were trivial. Of the 83 points in which a judge made an erroneous call, 70 of these were predicted errors (judges misperceived the position at which the ball bounced to be shifted in the direction of motion) and 13 were unpredicted errors. This bias (70/13) was statistically significant ($X^2(1) = 39.1$, $p < 0.0001$), demonstrating a substantial perceptual or reporting bias. Because 12 bounce positions were rated as being ambiguous (see Supplemental Figure S1A), and because our video raters were inherently subjective, we also separately analyzed those shots that had close-up video instant-replays (see Supplemental Figure S1B,C). During the televised games, every player challenge was accompanied by a video replay that included a close-up picture of the ball's bounce position. This provided an objective estimate of the ball's bounce location, independent of our observers. Of those shots that had accompanying replays (34 of the 83 above), 28 of these were predicted errors and six were unpredicted. This predicted error bias was still significant ($X^2(1) = 14.2$, $p < 0.001$). The same bias was also found in the 2008 Wimbledon championship. See Supplemental Figures S1 and S2 for more details. Because both players and referees should suffer from this bias, analyzing only the challenged calls [7], rather than analyzing all balls that bounce near a line, is likely to underestimate the magnitude of the perceptual error. In any case, the perceived shift in the position of a bouncing tennis ball is significant, and this sort of error could occur on any grass (Wimbledon) or cement court (US Open) but is less likely to happen on a clay court (French Open) simply because the clay permits inspection of the ball's skid mark on the surface and reduces reliance on referee motion perception.

Do humans really misperceive the position at which an object bounces or do tennis judges simply have a reporting bias? To test this in a more controlled setting, we conducted a psychophysical experiment (Figure 1C and Supplemental Figure S2). A moving dot was presented traveling along a trajectory that simulated motion toward or away from the observer on a computer screen (Supplemental Figure S2; see Supplemental Experimental Procedures for more details). The dot bounced at an unpredictable position and moment before continuing along its path (mimicking the trajectory of a tennis ball). A continuously visible horizontal line was presented on the screen and subjects were asked to fixate anywhere on the line and given the same instructions that professional tennis referees receive (see Supplemental Experimental Procedures). Although eye movements can cause mislocalizations of objects [8,9], tennis referees are asked to fixate or 'focus directly at the line' [10], potentially mitigating eye-movement related localization errors. Using a two alternative-forced-choice task, subjects reported whether the dot bounced below or above the bottom edge of the horizontal line. Supplemental Figure S2 shows that subjects displayed a bias in the perceived position of the dot's bounce: the perceived position of the bounce was shifted in the direction of motion ($X^2(1) = 24.8$, $p < 0.0001$, $X^2(1) = 5.3$, $p = 0.02$, for motion toward and away from the observer, respectively); motion toward the observer produced a stronger effect. This experiment mirrors exactly the perceptual bias observed in professional tennis referees' calls (Figure 1A,B): when asked to judge a transient portion of a moving object's trajectory (like the position of a bounce), subjects misperceive it as being shifted in the direction of the object's motion.

In a follow-up experiment, we presented two mirror symmetrical dots that were vertically separated and travelled toward each other before bouncing (Figure 1E, Supplemental Figure S3). Subjects perceived their bounce positions as being shifted in the direction of motion (Figure 1F), suggesting that eye movements per se are not entirely responsible (Supplemental Figure S3). The illusion revealed in these experiments is therefore more likely due to motion-induced position shifts [1], attention shifting [11], motion integration [12], or deblurring [13]. Each of these mechanisms would contribute in a similar manner and predict a directionally specific misperception in the localized bounce position, just as the data show.

There are several ways in which the systematic misperception of tennis ball location should influence player behavior. First, players should maximize their challenges: because the referee error rate is rather high for close calls, it is a suboptimal strategy to leave unused challenges. Second, because players are allowed to continue challenging referee calls as long as the challenges are correct, players should predominantly challenge those calls that are consistent with the perceptual error revealed here (Supplemental Figure S1). For example, when a ball is called "in", a player should usually not challenge the call, even when she believes it to be an incorrect call. Players should concentrate their challenges on balls that are called "out".

As it stands, the skill of challenging referee calls is intertwined with the skill of playing tennis itself; those players who make better use of their challenges benefit more. With full information about the perceptual errors that occur in tennis, such as those revealed here, all players could in theory benefit equally. Our results suggest that another way to level the playing field is for every shot in professional tennis to be objectively reviewed (by instant replay). If that proves prohibitively time-consuming, the rules allowing players to challenge referee judgments should be scrutinized at least, in light of the current findings. Importantly, perceptual errors by referees are not in themselves problematic, because the likelihood of misperception is equally distributed to both players. It is only when players are allowed to make challenges (and rewarded for their correct challenges) that a selective advantage can be introduced. If all else fails, perhaps professional tennis venues should follow the French, and universalize the clay court.

Supplemental Data

Supplemental data are available at http://www.current-biology.com/supplemental/S0960-9822(08)01098-1.

Acknowledgments

Thanks to Emilio Ferrer and Stephanie Zou. This work was supported by NIH EY18216.

References

1. Whitney, D. (2002). The influence of visual motion on perceived position. Trends Cogn. Sci. *6*, 211–216.
2. De Valois, R.L., and De Valois, K.K. (1991). Vernier acuity with stationary moving Gabors. Vision Res. *31*, 1619–1626.
3. Ramachandran, V.S., and Anstis, S.M. (1990). Illusory displacement of equiluminous kinetic edges. Perception *19*, 611–616.
4. Baldo, M.V., Ranvaud, R.D., and Morya, E. (2002). Flag errors in soccer games: the flash-lag effect brought to real life. Perception *31*, 1205–1210.
5. McLeod, P. (1987). Visual reaction time and high-speed ball games. Perception *16*, 49–59.
6. Regan, D. (1992). Visual judgements and misjudgements in cricket, and the art of flight. Perception *21*, 91–115.
7. Mather, G. (2008). Perceptual uncertainty and line-call challenges in professional tennis. Proc. Biol. Sci. *275*, 1645–1651.
8. Ross, J., Morrone, M.C., Goldberg, M.E., and Burr, D.C. (2001). Changes in visual perception at the time of saccades. Trends Neurosci. *24*, 113–121.
9. Schlag, J., and Schlag-Rey, M. (2002). Through the eye, slowly: delays and localization errors in the visual system. Nat. Rev. Neurosci. *3*, 191–215.
10. S.,Gerdes, and R., Kaufman, eds. (2008). Friend at Court: The USTA Handbook of Tennis Rules and Regulations. (White Plains, New York, USA: United States Tennis Association).
11. Baldo, M.V., and Klein, S.A. (1995). Extrapolation or attention shift? Nature *378*, 565–566.
12. Krekelberg, B., and Lappe, M. (1999). Temporal recruitment along the trajectory of moving objects and the perception of position. Vision Res. *39*, 2669–2679.
13. Burr, D. (1980). Motion smear. Nature *284*, 164–165.

The Department of Psychology, and The Center for Mind and Brain, University of California, Davis, California 95618, USA.
E-mail: dwhitney@ucdavis.edu