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STRAD α and MO25 α (Fig. 3 and table S2). In addition, at least 10 mutations involve residues required for catalysis or substrate binding (Fig. 3). Although these mutants properly assembled into complexes with STRAD α and MO25 α , these were devoid of catalytic activity (fig. S9 and table S2). Other mutations present in the activation loop (Ala²⁰⁵ \rightarrow Thr, Asp²⁰⁸ \rightarrow Asn), the α EF- α F loop (Thr²³⁰ \rightarrow Pro, Ser²³² \rightarrow Pro), and the CFT_L region (Pro³¹⁴ \rightarrow His, Pro³¹⁵ \rightarrow Ser, Pro³²⁴ \rightarrow Leu) did not affect the ability of LKB1 to assemble into active complexes. There are also a number of oncogenic mutations in solvent-exposed residues (Arg⁸⁶ \rightarrow Gly, Gln¹²³ \rightarrow Arg, Tyr²⁷² \rightarrow His, Asp²⁷⁷ \rightarrow Tyr) that do not affect complex assembly or activity (fig. S9 and table S2). Thus, out of 51 mutations analyzed, 18 formed complexes with STRAD α and MO25 α that showed LKB1 activity (table S2). Assuming these are cancer-driving rather than passenger mutations, some of these mutations may be involved in interacting with other regulators or substrates of the LKB1 pathway.

Our study reveals how LKB1 is activated. In addition to STRAD α binding, MO25 α plays a crucial role in stabilizing the LKB1 activation loop in a conformation required for phosphorylation of substrates. Thus, a previously unrecognized role of STRAD α is to promote interaction between MO25 α and LKB1. This represents a mechanism

by which kinases may be regulated allosterically, independent of activation loop phosphorylation. The LKB1 complex structure also shows how cancer mutations affect LKB1 function by impairing complex assembly, catalytic activity, and potential interactions with substrates or regulators. Finally, our findings provide insights into how certain pseudokinases may have evolved, by retaining active conformations that allow interactions similar to those by which active kinases bind their substrates.

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Supporting Online Material

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The Subtle Transmission of Race Bias via Televised Nonverbal Behavior

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Compared with more explicit racial slurs and statements, biased facial expressions and body language may resist conscious identification and thus produce a hidden social influence. In four studies, we show that race biases can be subtly transmitted via televised nonverbal behavior. Characters on 11 popular television shows exhibited more negative nonverbal behavior toward black than toward status-matched white characters. Critically, exposure to prowhite (versus problack) nonverbal bias increased viewers' bias even though patterns of nonverbal behavior could not be consciously reported. These findings suggest that hidden patterns of televised nonverbal behavior influence bias among viewers.

In contemporary Western culture, most people claim that they do not behave in a racially biased fashion, and America recently elected its first black president. Yet recent claims of a race-blind society are contradicted by studies of race biases, in which people exhibit more positive responses to one race than another (1–6). To the extent that race biases are communicated explicitly, egalitarian norms encourage observers to discount them as a valid source of knowledge (7, 8). For example, observers can consciously

debate and publicly denounce race-biased aggressive acts, verbal statements, and hiring procedures, thus resisting conformity to these explicit race biases. However, race biases are often com-

municated subtly via facial expressions and body language (2–6). Indeed, mounting evidence suggests that Americans' nonverbal behavior favors white over black persons (2, 4, 9–12). Because nonverbal behavior is “off the record” and can be difficult to identify unambiguously, exposure to nonverbal race bias may undermine norm-driven correction processes and hence may exert a social influence (13, 14). Specifically, exposure to nonverbal race bias, via evaluative conditioning, may cause perceivers to associate race with affect and thus exhibit race bias themselves (15–18). We examined the prevalence, subtlety, and impact of nonverbal race bias in four studies. We observed that nonverbal race bias occurs on television and that exposure to this televised bias accounts in part for white viewers' own race bias, as assessed with reaction-time and self-report measures. Moreover, patterns of nonverbal bias were influential even when they could not be consciously reported.

Table 1. Study 1: Featured (but unseen) character ratings by race. Means \pm SD; *t*(28).

Character rating	White character mean	Black character mean	<i>t</i> value	<i>P</i> value	<i>rpb</i>
Favorable nonverbal response	0.16 \pm 0.24	−0.04 \pm 0.28	2.08	0.047*	0.37
Favorable verbal response	0.17 \pm 0.20	0.04 \pm 0.34	1.35	0.19	0.25
Perceived attractiveness	4.88 \pm 1.16	4.74 \pm 1.04	0.35	0.73	0.07
Perceived sociability	4.79 \pm 0.66	5.14 \pm 0.88	−1.22	0.23	0.22
Perceived kindness	4.54 \pm 0.77	4.75 \pm 0.48	−0.90	0.38	0.17
Perceived intelligence	4.92 \pm 1.05	5.12 \pm 0.93	−0.56	0.58	0.10

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The first study examined whether nonverbal race bias existed across 11 television shows that reach millions of Americans on a weekly basis (19). To isolate race-based bias, we only examined popular television shows that included recurring white and black characters whose status could be roughly equated. We sampled at least three episodes from each of 11 shows that met our criteria (19). For each of 30 characters, we selected three 10-s clips from each episode according to a priori criteria. We selected the first clip from the first 5 min of each episode in which the character appeared in an interpersonal interaction (with a white person) lasting at least 10 s. These same criteria were applied to a clip from the “middle” 5 min and the last 5 min of each episode (nine clips in total).

We edited these clips to remove the audio track and the featured character. For example, the character Alexx of *CSI: Miami* was cropped out of her clips so that only the other characters could be seen—this procedure prevented any race-related demand characteristics (20). These cropped and silent video clips were shown to 23 white undergraduate judges who had not seen any of the 11 shows, as determined by responses to an e-mailed survey (21). For each cropped and silent clip, judges rated (with -3 to $+3$ scales) the extent to which the unseen character was treated positively and liked by the other characters (19). These ratings were averaged across judges to index the degree to which each featured character elicited favorable nonverbal responses from other characters (table S1).

Compared with black characters, white characters elicited significantly more favorable nonverbal responses (Table 1). On only 2 of 11 shows did black characters elicit (slightly) more favorable nonverbal responses than white characters. To examine whether white and black characters in these shows differed on variables other than race, 17 white student judges (who reported watching most of the 11 shows) rated each featured character for attractiveness, sociability, kindness, and intelligence. For each judgment, agreement among the judges was high (all interrater α values > 0.85), so scores for each character were averaged across judges (table S1). White and black characters did not significantly differ on any of these variables (Table 1). To examine whether white and black characters elicited different verbal responses, 13 white undergraduate judges rated (on a -3 to $+3$ scale) the transcribed verbal content of each clip for the extent to which the speaking characters treated featured characters favorably (table S1). White and black characters did not differ in the elicitation of favorable verbal responses (Table 1). Finally, even after controlling for all character traits and favorable verbal responses in an analysis of covariance, white characters elicited more favorable nonverbal responses than did black characters, $F_{1,23} = 4.30$, $P = 0.05$, $r_{pb} = 0.40$ (for correlations among character ratings, see table S2).

Nonverbal race bias was thus observed across 11 shows, each with an average weekly audience of 9 million, suggesting that many Americans are exposed to nonverbal race bias. These biases may occur for a variety of reasons: because actors spontaneously exhibit nonverbal bias, because biased nonverbal behavior is written into scripts, and/or because directors persuade actors to change their nonverbal behavior. Regardless, the bias appears on a number of popular television shows and thus may influence viewers. In study 2, we examined whether natural exposure to nonverbal race bias via television was related to viewers' own race associations. Exposure to subtle covariation between race and affect on television should produce associations in viewers [perhaps via evaluative conditioning (15–18)]. The implicit association test (IAT) (3) was used to assess viewers' race associations. Although there is debate about the extent to which IAT scores index implicit racial prejudice versus cultural knowledge (22–25), the IAT does measure psychological associations that predict race-related thought and behavior (26, 27). (See study 4 for a replication with a different measure.)

For study 2, we computed nonverbal bias scores for each of the 11 shows by subtracting the favorable nonverbal response score for the black character(s) from that of the white character(s). Hence, higher numbers indicated more prowhite bias for a show ($M_{Show} = 0.10$, $range_{Show} = -0.08$ to 0.43). Exposure to nonverbal race bias scores were calculated for each of 53 white undergraduate participants by first determining which of the 11 shows they watched (via survey) and then averaging the nonverbal race bias scores for these shows [for this calculation, see (19)]. In an ostensibly separate study, participants completed a race IAT in which they identified faces as white or black and words as positive or negative—on trial block “w-p,” participants used the same key to respond {“white” or “positive”} and another key to respond {“black” or “negative”}, whereas on trial block “b-p,” the pairings were {“black” or “positive”} and {“white” or “negative”}. IAT scores were computed as the standardized difference in reaction times between block w-p ($M = 746.15$) and block b-p ($M = 993.81$) such that higher

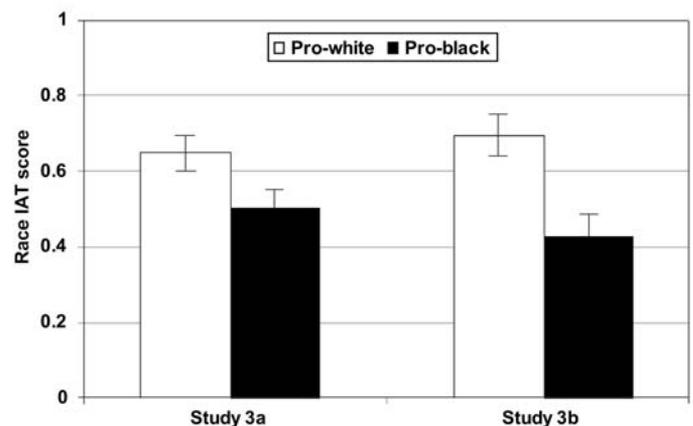
scores indicate faster responses to white-positive and black-negative than to white-negative and black-positive (28) (table S3).

As expected, more exposure to nonverbal bias was associated with greater IAT scores [$r(51) = 0.28$, $P = 0.047$]. To examine the possibility that the explicit verbal content on these shows was confounded with and accounted for effects of nonverbal content, we calculated verbal race bias scores for each show. We subtracted favorable verbal response scores (study 1) for black characters from those for white characters. These verbal race bias scores were averaged across each participant's regularly watched shows to form an “exposure to verbal bias” score. Exposure to verbal race bias was not significantly related to IAT scores [$r(51) = 0.15$, $P = 0.27$].

Alternatively, exposure to any nonverbal bias (e.g., toward attractive characters) might account for the study 2 findings. With the character ratings from study 1, we computed indices of exposure to nonverbal biases unrelated to race. For example, each character's favorable nonverbal response score (study 1) was multiplied by his or her perceived attractiveness score, and these scores were averaged within each show. Thus, shows with higher scores depicted especially positive nonverbal behavior directed toward attractive (versus unattractive) characters. We averaged these scores across the shows watched by each study 2 participant; the same procedure was followed for perceived sociability, kindness, and intelligence. Exposure to these alternative nonverbal biases was unrelated to viewers' race associations—this was true for attractiveness [$r(51) = 0.05$, $P = 0.73$], sociability [$r(51) = 0.16$, $P = 0.25$], kindness [$r(51) = 0.06$, $P = 0.70$], and intelligence [$r(51) = -0.11$, $P = 0.45$]. Finally, a partial correlation (pr) with nonracial biases and verbal race bias as covariates revealed a still-significant relation between exposure to nonverbal race bias and IAT scores [$pr(46) = 0.29$, $P = 0.048$].

The correlational design of study 2 leaves open several possibilities for causality, including that exposure to nonverbal bias influenced viewers' own bias or that viewers' own bias caused them to watch nonverbally biased programs. The

Fig. 1. Mean IAT scores in studies 3a and 3b as a function of exposure to nonverbal bias (prowhite or problack exposure). Error bars represent SEM.



focus here was on social influence, so we conducted several experiments to assess the causal influence of exposure to nonverbal race bias. In studies 3a ($n = 62$) and 3b ($n = 35$), white participants were exposed to one of two sets of silent video clips. In both experiments, the “pro-white” set depicted white characters eliciting favorable nonverbal behavior and black characters eliciting unfavorable nonverbal behavior (6). The “problack” set depicted the opposite pattern (these patterns were confirmed by independent judges) (19). To control for potential confounding variables in study 3a, the same characters appeared in the prowhite and problack sets. In study 3b, the prowhite and problack sets were matched for character attractiveness, sociability, kindness, and intelligence, as confirmed by independent student judges (table S4).

The procedure and measures were identical across studies 3a and 3b. In both studies, after exposure to one of the two sets of video clips (prowhite or problack), participants completed what they thought was a separate study but was actually the same IAT used in study 2 (for IAT calculations and component means, see table S3). As expected, participants exposed to the prowhite clips exhibited significantly higher (prowhite) IAT scores than participants exposed to the problack clips, and this was true for both study 3a ($F_{1,58} = 3.91, P = 0.05, rpb = 0.25$) and study 3b ($F_{1,31} = 4.75, P = 0.04, rpb = 0.36$) (Fig. 1). Thus, exposure to nonverbal race bias influenced perceivers’ own race associations.

We have argued that nonverbal race bias exerts a particularly subtle influence because perceivers are unlikely to be aware of its presence. This does not mean that perceivers should have difficulty identifying nonverbal behavior per se but rather that they should have difficulty identifying a pattern of nonverbal race bias. Accordingly, we investigated whether people could consciously identify patterns of nonverbal race bias across each set of clips from study 3b. Twenty-two white participants were told that there was a hidden pattern across silent video clips which they then watched—half watched each set (prowhite or problack). After viewing these clips, participants were asked to indicate whether black characters had been treated better than white characters or the converse. Judgments were not different from chance (50%)—in each condition, 45% guessed that the clips were “problack.” Hence, participants were unable to report the pattern of nonverbal behavior across clips, which suggested that nonverbal race bias exerts an unconscious influence.

In a fourth study, we further examined the causal influence of nonverbal race bias established in studies 3a and 3b. We added a control condition to assess the polarity of this influence; the control condition included clips from each of the other two sets and depicted equally positive nonverbal behavior directed toward white and black characters (19). Additionally, an affective priming measure (4, 29) replaced the IAT. This measure assessed the degree to which sub-

liminal images of black, white, or Asian faces sped responses to positive versus negative target images. For the 56 white participants in this study, differences in reaction time to positive versus negative objects were calculated for each prime (black, white, and Asian) to index affective associations (29) (for component means, see table S5).

A 3 (nonverbal bias) \times 3 (prime race) analysis of variance (ANOVA) revealed only a significant interaction ($F_{4,106} = 3.13, P = 0.02$) (Fig. 2). A priori contrasts revealed that white associations were more positive for participants exposed to prowhite nonverbal bias than to problack nonverbal bias ($F_{1,106} = 6.71, P = 0.01$) or to the control condition ($F_{1,106} = 9.72, P = 0.002$), whereas the last two conditions did not differ ($F_{1,106} = 0.09, P = 0.77$). Black associations were more positive for participants exposed to problack nonverbal bias than to prowhite nonverbal bias ($F_{1,106} = 4.77, P = 0.03$) or to the control condition ($F_{1,106} = 4.62, P = 0.03$), whereas these last two conditions did not differ ($F_{1,106} = 0.001, P = 0.97$). Asian associations did not differ by nonverbal bias condition (all F values $< 1, P$ values > 0.36). Hence, the effects of nonverbal race bias seemed to be (i) specific to the races targeted in the nonverbal bias, (ii) of similar magnitude for prowhite and problack nonverbal bias, and (iii) largely due to the increased positivity of measured associations.

To examine whether nonverbal bias influenced feelings for particular characters, participants were asked (after the exposure phase) to rate how much they liked each character—the difference between liking for white ($M = 4.21$) and black characters ($M = 4.54$) indexed “relative liking” (19). An ANOVA revealed a main effect ($F_{2,53} = 13.65, P < 0.001$). Participants in the control condition exhibited less relative liking ($M = -0.33$) for white characters than those in the prowhite condition ($M = 0.46, P = 0.02$), and less relative liking for black characters than those in the problack condition ($M = -1.09; P = 0.03$) (Bonferonni post hoc analyses). Hence, self-reported affect toward white and black characters was influenced by exposure to nonverbal bias. Moreover, greater relative liking for white over black characters was correlated with more positive white associations on the priming task (Table 2). Indeed, positive white associations accounted in part for the relation between exposure to prowhite nonverbal bias (versus the control) and relative liking (19).

Participants also completed a conventional measure of racial prejudice (the “attitudes toward blacks” self-report survey) (30). An ANOVA revealed that scores differed by exposure condition ($F_{2,53} = 3.21, P = 0.048$). Those in the problack nonverbal bias condition exhibited significantly lower self-reported racial prejudice ($M = 1.83$) as compared with the prowhite condition [$M = 2.22, t(33) = 2.08, P = 0.04$], and the control condition [$M = 2.26, t(33) = 2.66, P = 0.01$]. Hence, exposure to problack nonverbal bias mitigated self-reported racial prejudice.

Fig. 2. Mean race-based associations as a function of exposure to nonverbal bias (prowhite exposure, problack exposure, or control condition). Higher numbers on the y axis indicate faster responses to positive (versus negative) targets. Error bars represent SEM.

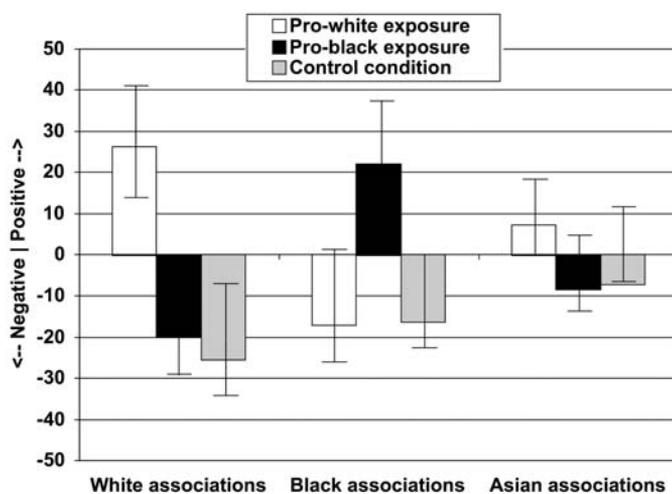


Table 2. Study 4: Correlations among measures. P values in parentheses. More positive associations indicate faster responses to positive (versus negative) target images following a race prime. Character ratings index liking for white minus black characters. $n = 53$.

Measure	White associations	Black associations	Asian associations	Character ratings
White associations				
Black associations	0.25 (0.07)			
Asian associations	0.01 (0.96)	-0.10 (0.46)		
Character ratings	0.33 (0.01)	0.04 (0.76)	0.05 (0.74)	
Attitudes toward blacks	0.10 (0.44)	0.01 (0.97)	0.02 (0.88)	0.24 (0.08)

Perhaps it is not surprising that exposure to prowhite nonverbal bias failed to increase self-reported racial prejudice; strong norms against racial prejudice may place a ceiling on self-reports of racial prejudice. Nonetheless, the results of study 4 suggest that exposure to nonverbal bias influenced (i) race associations, (ii) feelings toward particular white and black persons (television characters), and (iii) self-reported racial prejudice.

In conclusion, Americans are exposed, via television, to nonverbal race bias, and such exposure can influence perceivers' race associations and self-reported racial attitudes. Nonverbal behavior that communicates favoritism of one race over another can be so subtle that even across a large number of exposures, perceivers are unable to consciously identify the nonverbal pattern. Yet despite (or perhaps because of) this subtlety, exposure to nonverbal race bias may transmit race bias to perceivers.

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19. Materials and methods are available as supporting material on Science Online.
20. Demand characteristics inform participants about the purpose of the study and thus influence responses. Here, knowledge of target characters' race might have led participants to infer that we expected black characters to be treated poorly and thus could have altered participants' ratings. By cropping out the target character, we avoided this demand characteristic.
21. All studies were approved by the Tufts University Internal Review Board (IRB). Unless otherwise noted, participants in all studies were debriefed, paid, and thanked and then were excluded from participating in other studies.
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Supporting Online Material

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